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MARCH, 1958

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KEYS TO THE ORDERS, FAMILIES AND GENERA OF HEPATICAE OF AMERICA NORTH OF MEXICO

RUDOLF M. SCHUSTER*

The absence of any ready means of identifying the genera of North American Hepaticae has limited the development of interest in the group. The keys presented here attempt to satisfy this need. These keys fall into two categories (*a*) synoptic keys to classes, orders, suborders and families and (*b*) under each order and/or suborder artificial keys to the genera, if more than one genus is included. The first type of key necessarily represents a synthesis of the most "typical" characters of the various groups, arranged in a systematic fashion. By its very nature, a synoptic key cannot take into account isolated exceptions or deviant taxa. However, such a synoptic key has the advantage of giving some idea of the salient characteristics and limits of the various groups. By contrast, artificial keys are rightly concerned only with the practical problem of identification. In the synoptic keys to families I have indicated, in parentheses, the genera included in each family. Therefore, in cases of doubt, a specimen can be run through both the artificial and synoptic keys, using one key as a check on the other. A number of other pertinent points deserve mention in this connection:

(1) I have indicated, throughout these keys, various "traps" into which the unwary may fall. Similarly, exceptions to the rule are indicated. In

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some instances, special techniques of preparation may be necessary for key characters to be properly ascertained; such cases are also noted. Wherever special guidance may be needed, explanatory material is introduced in annotations which are given in Appendix II.

(2) The arrangement, particularly into families, followed here is essentially that in Schuster (1953), with a few slight exceptions. This system embraces some elements in various recent classifications, notably those of Verdoorn (1932), Evans (1939), Buch (1936a), Müller (1951-56), and, like them shows little or no similarity to the classification adopted in the recent work of Frye and Clark (1937-47). This is unfortunate, since that work is both readily accessible and widely used, but the writer fails to see any way of avoiding it. The conceptual bases underlying the writer's classification will be presented elsewhere.

(3) Because the concept of genus is no more stable now than in the past, there are numerous discrepancies in the literature as to generic limits. For example, all recent works on the Lophoziaceae, unless they represent uncritical compilations, differ from each other in some respects (see Schuster, 1951). In general, the problems involved have been concerned largely as to whether a group of species, or even an individual species, should be segregated as a distinct genus or left as a section or subgenus within a larger, "portmanteau" genus. I have used, in this and other works, the arbitrary criterion that extensive intergradation between groups of species invalidates them as genera. Subgenera may be recognized where such transitions occur, but genera should have reasonably clear limits. Since what constitutes "reasonably clear limits" is and will remain a subjective matter, it seems reasonable that no final agreement will be reached on certain points. Fortunately, these areas of disagreement are rather few and occur chiefly in the Lejeuneaceae, Lophoziaceae and Jungermanniaceae. In these groups I have given, in the annotations (Appendix II), keys to separate the groups considered here to be subgenera, but which sometimes are given as genera. Outright synonyms are placed within parentheses. Genera and subgenera which include single species in our area have these species indicated, in parentheses, after the generic name.

(4) In order to guide the student to recent interpretations of various difficult groups, I have indicated, in the annotations, references to a large number of recent papers (all published since 1937) in which further guidance may be obtained. This technique serves to orient the student to all pertinent literature modifying the concepts prevailing in American literature antedating the last decade.

(5) As is evident to any student with previous experience in the Hepaticae, these keys owe much to various earlier works, particularly to Macvicar (1926), Müller (1905-16, 1951-56), Buch (1936), Jensen (1915), etc. At various points, however, I have introduced new features and new criteria, such as the nature of the rhizoid distribution pattern in leafy Hepaticae, type of asexual reproductive patterns, oil body and other cytological characteristics, stem anatomy, etc. The keys are designed for accuracy but not necessarily for speed. Where two or three good separating characters are available, I have used them rather than single opposed characters. Primary key characters are used first in each couplet, supplementary characters last. In spite of a certain loss in continuity, this technique serves to emphasize the most salient differential criteria.

(6) The keys are strictly dichotomous. Furthermore, every attempt has been made to construct them so that a taxon will key out once, rather than

in a variety of places. Unfortunately, the extreme polymorphism of several genera (*Plagiochila, Nardia*) makes it necessary to key them out two or more times. In such cases, after the generic name, I have indicated this fact either by giving, in parentheses, the species keying out at this point, or, if the species are numerous, by stating "in part."

(7) Critical features in the keys are occasionally italicized. In the case of couplets utilizing more than a single pair of characters, the initial opposed characters are to be regarded as the most salient. Cytological characters involving study of living material are, in so far as possible, relegated to a secondary position. It should be recognized, however, that in some groups they afford by far the best and most evident features for separating genera.

(8) Several plates, at the end of this treatment, illustrate key characters within the difficult Jungermanniales (and, in a few cases, Metzgeriales). These figures are referred to as, for example, (3:10), meaning fig. 3, individual fig. 10.

(9) In the Order Jungermanniales, the largest and by far the most difficult group, identification is often complicated by the fact that the plants lack all trace of sex organs or sporophytes and reproduce only by asexual means. Such asexually reproducing plants are often so atypical that they are not readily identified and may be almost unrecognizable (as in small gemmiparous plants of *Eremonotus helierianus*). It was thus deemed necessary to give a key to asexually reproducing material which would include *only* those genera (and species) in which specific asexual patterns of reproduction exist. Such a key affords virtually the only means for identifying certain taxa; it also affords by far the easiest means of identifying various species regularly reproducing asexually.

(10) Several genera and subgenera have been reported as new to North America since the publication of Frye and Clark (1937-47) or represent recent segregates which the writer feels compelled to recognize. In such cases, attention is called (in an appropriate annotation) to the publication in which mention is made of the regional discovery of these groups or in which these groups are described. In other cases, incorrect generic assignments currently exist (for example, *Lepicolea fryei* is not a *Lepicolea*), or genera (such as *Dichiton*) are reported from America that do not occur there. The reasons for such taxonomic changes and exclusions will be better treated elsewhere; a brief basis for the stand taken here is indicated in the annotations.

(11) Finally, the writer is quite aware that these keys will prove to have their imperfections. Dr. Virginia S. Bryan, Mrs. Ardith Brask Johnson and Mr. Harry Williams deserve much credit for having conscientiously used the keys to the leafy taxa and suggesting corrections and improvements. Since these keys will form the foundation for those to be formulated for the writer's text on *The Hepaticae and Anthocerotae of Eastern North America*, he will appreciate receiving suggestions for their improvement and also material which fails to key out readily. Finally, it must be kept in mind that no key can be made for wholly juvenile plants, or plants growing temporarily under such atypical conditions that their normal form is not realized. *Conocephalum conicum*, growing submerged, will produce forms with vestigial pores and air chambers. No key can take into account such monstrosities!

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CONSPECTUS OF CLASSES AND ORDERS[1]

1. Gametophytic cells each with several to many chloroplasts, with or without oil bodies; plants thallose or leafy, without stomata; capsules not linear, usually not 2-valved, without a columella (1:2; 5:3-5, 7), without stomates. Class HEPATICAE 2

2. Rhizoids (if present) all smooth; plants leafy or thallose (1:1, 6; 2:1-8; 6:3, 7), if thallose ± delicate and translucent, without air chambers or canals 3

3. Sporophyte with a distinct seta and foot (1:2; 5:4); capsule wall dehiscent, 2-8-stratose (except *Haplomitrium*), usually valvate; gametophytic cells each usually bearing several oil bodies; archegonia and antheridia not individually surrounded by a delicate, tubular to obpyriform involucre (1:14; 5:1-2, 5-6); spore tetrads separating before exospore is completely developed, the spores thus rounded, normally without differentiated inner faces; elaters present, with spiral thickenings 4

4. Plants clearly leafy (1:6; 2:1-8); archegonia terminal on branches or main axes, not becoming dorsal on plant (5:1-9) 5

5. Plants isophyllous, the three rows of leaves transverse, identical, unlobed; perianth and perigynium absent, the calyptra sheltering the sporophyte (1:5); rhizoids absent; sporophyte with wall unistratose, each cell with a longitudinally oriented band; seta very massive (7:1); no asexual reproduction. Order 1. CALOBRYALES (Haplomitrium) ..... p. 5

5. Plants normally anisophyllous, with two obvious rows of lateral leaves, and a third row of "underleaves" which are somewhat to greatly reduced (2:9; 3:5; 5:6) or absent (2:4, 6; 3:3) (rarely, in bilobed-leaved species, nearly as large as the leaves; 2:7); usually with rhizoids (2:4, 7; 5:2); perianth (1:6, 8, 10, 12) or

perigynium (5:3-5, 7), or both, usually present and protecting sporophyte, the calyptra not naked and massive; sporophyte with wall 2-8-stratose, the thickenings transversely oriented, several per cell; often with asexual reproduction. Order 2. JUNGERMANNIALES ..... p. 5

4. Plants thallose (1:15; 6:3, 7) (*Fossombronia* clearly leafy, 1:1; with purple rhizoids!); archegonia (and antheridia) dorsal on surface (1:1) or on branches of the plant (1:14-15). Order 3. METZGERIALES ..... p. 30

3. Sporophyte with foot and seta short, obsolete; capsule cleistocarpous, without lines of dehiscence, the wall 1-stratose; cells without oil bodies, or only isolated cells with a single one; elaters obsolete, minute spherical cells, without spirals; archegonia and antheridia surrounded by individual involucres; spore tetrads not, or tardily separating, or if separating inner spore faces differentiated. (Plant ± leafy, or bearing leaf-like scales.) Order 4. SPHAEROCARPALES ..... p. 32

2. Rhizoids abundant, partly smooth, partly with peg-like thickenings in the walls; plants thallose, opaque, usually with distinct pores and air chambers; sporophyte with seta short or absent; capsule wall 1-stratose; oil bodies absent, or single in isolated, scattered cells. Order 5. MARCHANTIALES ..... p. 32

1. Gametophytic cells normally with a single, large chloroplast, without oil bodies; plants thallose, the undersurface of the thallus often with ± distinct stomata, opening into slime chambers; sporophytes with linear capsules splitting into 2 valves, with columella and stomates usually well developed. Class ANTHOCEROTAE. Order 1. ANTHOCEROTALES ..... p. 36

Class HEPATICAE

Order 1. CALOBRYALES

Only the genus *Haplomitrium* in our area.

Order 2. JUNGERMANNIALES

I. CONSPECTUS OF THE SUBORDERS OF JUNGERMANNIALES

1. Archegonia generally (10)12-20(24) per gynoecium; leaf insertion varying from transverse (2:1, 8; 3:2-3) to succubous (2:5) to succubous-complicate (3:11-14) or simply incubous (4:1-3), never incubous-complicate (*i.e.*, complicate-bilobed with the larger dorsal "half" incubously shingled, the line of insertion not curved to stem apex dorsally and ventrally); branching variable: intercalary (2:1, 4) or terminal, if terminal the branch always replacing the ventral half of a leaf (2:1, 3, 5, 7, 8); asexual reproduction often by means of fasciculate, few-celled gemmae (6:8, 10-12) (never by discoid broodbodies produced singly), less often by caducous or fragmenting leaves; developing sporeling or gemmaling usually forming a ± filamentous protonema or at least not a flat, thallose one; sporophyte with seta usually elongate, normally exserting the sporangium; perianth often reduced (1:7 pt) or absent (5:8), often partly or wholly replaced by a perigynium (5:3-5, 7); the stem peripheral to archegonia often proliferating after fertilization, forming a "calyptral perigynium" (5:1, 7) 2

2. Leaf insertion varying from transverse (2:1, 7; 3:2) to succubous (2:3-5; 3:4-5); the leaf-planes generally succubously oriented (occasionally complanate (3:11-14); then with at least ventral half of line of insertion running towards stem-apex); generally able to develop 1-2-celled gem-

mae (6:8-12); ventral merophytes usually narrow, rarely as much as 0.25 the circumference of the stem in extent (3: 3v, 13); rhizoids always more or less frequent (3:10; 3:3)—potentially arising from any postical stem cell, hence not restricted to the bases of underleaves[2]; leaves most commonly 2-0-lobed (only a few primitive forms able to develop 3-4-lobed leaves) (1:3, 10; 2:1-5, 8; 3:1-4).....JUNGERMANNINAE

2. Leaf insertion (in our genera, except in *Trichocolea*) varying from transverse to incubous: the dorsal end of the line of insertion normally slightly to strongly inclined to stem apex (4:1-3); rarely able to develop gemmae; ventral merophytes always broad: 0.25-0.33 the stem-circumference in extent (4:3, 15); rhizoids often rare and occurring only on the bases of a few underleaves on each stem (4:11-12), always restricted to small, specialized, rhizoid-initial regions at the bases of the underleaves.[3] Leaves (except in *Calypogeia*) generally or often 3-4-lobed, the dorsal lobe generally the larger (4:1, 4; 6:5).....PTILIDIINAE

1. Archegonia 1-4, or primitively 8-10 (12) per gynoecium. Leaf insertion and orientation incubous-complicate: the larger dorsal "half" of the leaf incubously shingled and inserted (4:5, 7, 10), the insertion running toward stem-apex, the reduced ventral "half" bent under and ± hidden under the dorsal "half" (4:4, 14) (in exceptional instances the ventral "half" obsolete[4]; branching normally entirely terminal (2:6) (intercalary branches, from axils of leaves or underleaves, absent); asexual reproduction diverse (where present), often by means of discoid broodbodies which are produced singly (6:14), never by means of fasciculate 1-2-celled gemmae; sporelings and gemmalings usually developing a transitory bilateral, flat, thalloid protonema; sporophyte with seta always short, typically hardly exserting the capsule beyond perianth; perianth (1:8, 12) always well developed, never subtended by a perigynium; sterile archegonia (if present) never elevated after fertilization by proliferation of shoot tip within the perianth, thus without a "calyptral perigynium." Spores usually large (20-50 μ in longer diameter), their diameter usually 3-8× that of elaters 3

3. Apical cell tetrahedral, cutting off 3 rows of segments (3:6-7; 4:6, 15), thus shoots with distinct ventral merophytes (rarely reduced in minute, reduced taxa to a width of 1 cell). Leafy shoots normally freely developing rhizoids which are confined to underleaf-bases (4:12) or to lobuli of leaves (2:6); without basal rhizomatous shoots; branches lateral: either replacing ventral half of leaf (4:14) or originating below leaf at base of keel (2:6); asexual reproduction often present (6:13-14); sporophyte with capsule wall 2-4-stratose; spores usually precociously germinating within capsule wall; leaves with dorsal half never bilobed (4:5, 13); ventral half not provided with a complex valvular apparatus (4:4, 14). 4

4. Rhizoids restricted to small area on the lobules, absent on the stem (2:6); stem without any trace of underleaves (not even slime papillae!), but ventral merophytes remaining broad (2:6; 4:4, 8); perianth truncate at the wide mouth, dorsoventrally compressed; cells with 1-2 large, plate-like, granular opaque oil bodies; capsule ovoid-cylindrical. .....RADULINAE (Radulaceae; only the genus *Radula*)

4. Rhizoids restricted to small areas on the stem (4:12), at the bases of the underleaves (in a few genera, with suppressed underleaves, restricted to point of suppression); perianth various (1:8-9, 12-13), but

never broad at the mouth, usually narrowed into a beak; capsule spherical. ..... PORELLINAE

3. Apical cell cutting off only *2* rows of segments, the shoots thus lacking ventral merophytes (hence without trace of underleaves); leafy shoots without rhizoids, these confined to basal rhizomatous shoots; branches only from near dorsal base of normal leaf; without asexual reproduction; sporophyte with capsule wall very firm, 8-stratose; elaters free, tapering on both ends, *2*-spiral; spores never(?) precociously germinating. Leaves often with dorsal half bilobed; ventral half typically conchiform, with a complex valvular closing apparatus; (perianth cylindrical to fusiform, deeply pluriplicate, narrowed to the ciliate-dentate mouth)..... PLEUROZIINAE (Pleuroziaceae; only the genus *Pleurozia*)

The preceding division of the Jungermanniales into five suborders is novel. The basis for this division is briefly outlined in Appendix I.

II. CONSPECTUS OF THE FAMILIES OF JUNGERMANNIALES[5]

1. Leaves divided virtually to base into *3*-4 filiform segments (6:5), or deeply lobed and fringed on the lobes with uniseriate cilia (4:1, 3); the leaf lamina then strongly resolved into numerous cilia; underleaves similar to leaves, nearly as large as leaves, similarly lobed or fringed; rhizoids (when present at all) restricted to underleaf bases; leaves incubous (4:1-3; 6:5) or transverse (succubous only in *Trichocolea*). (Suborder PTILIDINAE in large part). 2

2. Leaves and underleaves deeply lobed and fringed with cilia (4:1, 3); leaves distinctly incubously shingled; chief leaf lobes 6 or more cells broad; coarse, robust, 1-3-pinnately branched plants; rhizoids virtually absent; capsule wall 4-8 cell layers thick; seta of numerous epidermal cell rows (7:1-2)..... 3

3. Cells with bulging trigones, the cuticle smooth; perianths well developed, without a perigynium; plants ± reddish-brown or brownish; capsule wall 4-stratose..... PTILIDIACEAE (*Ptilidium*)

3. Cells without trigones, the cuticle striolate; perianths absent, replaced by a fleshy, paraphyllose perigynium lying in the axis of the main stem; plants whitish to yellowish-green; capsule wall 7-8-stratose, the epidermal layer of large, pellucid cells, lacking thickenings. ..... TRICHOLEACEAE (*Trichocolea*)

2. Leaves and underleaves divided virtually to base into (*2*)3-4 subequal capillary or filiform lobes or cilia (6:5), at most 2-5 cells broad at the very base; plants small to minute, with transverse leaves, brownish- to whitish-green; perianths present, crenulate or ciliate to setulose at mouth. Capsule wall *2*(-3)-stratose; seta with only 8(9-10) epidermal cell rows (7:5-6)..... 4

4. Perianths terminal on main shoots, not sharply trigonous; leaves typically 4-lobed almost to the base, the lobes uniseriate (6:5) to base; flagella absent; branches lateral, from the ventral half of the segment; with gemmae occasionally developed (6:4). ..... BLEPHAROSTOMACEAE (*Blepharostoma, Lophochaete*)[6]

4. Perianths terminal on short (rarely long) ventral shoots, more or less trigonous; leaves *2*-4-lobed to near base, but the bases of some lobes *2* cells broad; flagella (often postical, at other times terminal) often

present; never developing gemmae; seta with 8 epidermal, many small inner cell rows (*7*:5-6).

.....LEPIDOZIACEAE[7] (*Microlepidozia, Telaranea*)

1. Leaves extremely diverse, often lobed or dentate (*2*:1-5, *3*:1-5, 11; 5:6) but never divided to the base into 3-4 lobes, or resolved into numerous filiform segments (rarely with marginal teeth or cilia that may be uniseriate for a length of 2-5 cells or more, *2*:5)..... 5

5. Leaves (in dorsal aspect) clearly incubously shingled and oriented: the dorsal leaf margins all lying nearest the stem apex; rhizoids (often absent except very locally on some stems) restricted either to the bases of the underleaves (4:12) or to a small area on the ventral fold (lobule) of the leaf (*2*:6); underleaves usually large.[8]..... 6

6. Leaves simple: either variously lobed or entire, but never with the posterior margin elaborated as a lobule that has become folded under (and hidden under) the dorsal portion of the leaf. Sexual branches (at least) postical and intercalary. Sporophytes with capsules very long-stalked. (Suborder PTILIDIINAE, in part)..... 7

7. Plants freely, regularly terminally branched; leaves 3-4-lobed or dentate (at least on the most robust shoots; occasionally only 2-dentate, but plants then strongly brownish-pigmented); underleaves more or less dentate or lobed; plants freely producing flagella (either postical or terminal); without gemmae; perianths present (but rarely developed); cells ± collenchymatous.

.....LEPIDOZIACEAE (*Lepidozia, Bazzania*)

7. Leafy shoots simple but bearing frequent postical, intercalary branches from the underleaf axils; leaves entire (or delicately bidentate at apex); plants whitish to greyish-green, pellucid, with large cells (over 30 × 35 μ in leaf middle) with trigones none or very small; with obviously segmented oil bodies; plants lacking flagella, but often with erect, filiform gemmae-bearing shoots; perianths absent, but developing a postical, hairy perigynium.

..... CALYPOGEIACEAE (*Calypogeia*)[9]

6. Leaves complicate-bilobed: divided into a larger, incubous dorsal lobe, beneath which is hidden a more or less modified ventral lobe ("lobule"), often inflated or otherwise specialized (*2*:6; 4:4-5, 13-14; 6:13). Branches all lateral, of *Frullania*- or *Radula*-type (*2*:6; 6:13). Plants never developing flagella nor provided with 1-*2*-celled gemmae 8

8. Underleaves lacking (*2*:6; 4:8) branches uniformly arising in association with an unmodified leaf (*2*:6); rhizoids absent from normal, leafy stem; perianths never beaked at apex: either spade-like and truncate distally, or pluriplicate and ciliate at mouth; (elaters free, bispiral; capsule ovoid, 4-valved to base)..... 9

9. Large, purplish to brownish plants 2-5 mm. wide × 5-20 cm. long; rhizoids absent on leafy stems, confined to reduced-leaved shoots; leaves with lobules largely free from stem, strongly inflated, with a complex closing mechanism; leaf lobes bilobed and toothed; cells with coarse trigones and 8-12 oil bodies each; lateral branches *from antical margin* of anterior portions of merophytes, *arising from near antical base of leaf*; perianths deeply 4-10-plicate, ciliate

at mouth; archegonia 1-2 per gynoecium; capsule short-ovoid, the thick wall 8-stratose.

.....(Suborder PLEUROZIINAE) PLEUROZIACEAE (*Pleurozia*)

9. Medium-sized green to yellowish, rarely brownish plants 0.5-2.5 mm. wide × 1.5 cm. long; rhizoids arising from lobules of leaves (2:6); lobules ± connate to stem, usually longly so, not or hardly inflated (2:6; 4:4, 7-8), open along their free margins; leaf lobes rounded and entire (4:4-5); cells with small to large trigones, with only 1-2 very large, plate-like oil bodies; branches of the *Radula*-type only: lateral, arising posterior to an unmodified leaf (2:6). Perianths flattened dorsoventrally, truncate at the wide, entire mounth; archegonia 5-7 (10-16) per gynoecium; capsule ovoid-cylindric, the wall 2-stratose.

.....(Suborder RADULINAE) RADULACEAE (*Radula*)

8. Underleaves large and conspicuous (4:12, 14), with rhizoids restricted to their bases;[10] perianths beaked or narrowed at apex, not longly ciliate (1:8, 12); (capsule spherical, with broad valves).

..... 10

10. Ventral lobes (lobules) not inflated, similar in appearance to the undivided underleaves (4:14); plants large (2-5 mm. wide), olive- to blackish-green; perianths at most conically pointed near the mouth, which is ciliate and not beaked; branching only of the *Frullania*-type; capsules with wall 3-4-stratose, with valves not completely opening, often tearing, not bearing the elaters on their inner surfaces, the elaters free, tapering on both ends.

.....PORELLACEAE (*Porella, Ascidiota*)[11]

10. Ventral lobes (lobules) typically inflated, very different in appearance from the underleaves (which are sometimes absent) (1:12; 6:13); plants small, 0.5-2.5 mm. wide, yellow-green to green to reddish-brown or deep green; perianths 3-5-keeled (1:8-9), ending in a distinct beak, occasionally with supplementary ridges (1:12-13); capsules with wall 2-stratose, 4-valved to near base, the valves bearing attached on their apices the trumpet-shaped elaters.....11

11. Leaves divided virtually to base: the lobules almost free from the lobes, the keel between the two usually vestigial, lying usually almost parallel with stem and attached to it only by a very narrow fold; lobules galeate, inflated so that the morphologically abaxial surface of the leaf forms the inner lining of the lobule; plants deep green or brownish to reddish- or purplish-brown; perianths (in our species) flattened, 3-4-carinate (occasionally with weaker supplementary ridges); branches of the *Frullania*-type; seta with numerous epidermal cell rows, at maturity not articulated.

.....FRULLANIACEAE (*Jubula, Frullania*)

11. Leaves not divided to base: the lobules with their longer axis parallel to posterior leaf-margin (the keel elongated), usually broadly attached to the stem (1:12; 6:13); lobules (except when reduced in size) inflated, pouch-like, inflated so that the morphologically abaxial surface of the leaf forms the outer surface of the lobule (6:13); plants usually yellowish-green, sometimes with brownish (but never reddish!) pigmentation; perianths (in our species) variously from 4-5-16-carinate (1:8-9, 12-13). Branches all (or predominantly) of the *Radula*-type; seta articulated at

maturity, with 12-16 epidermal rows and 4 inner rows of cells (7:7-8).....LEJEUNEACEAE (*ca.* 20 local genera)[12]

5. Leaves clearly succubously shingled (or succubously-complicate) or transverse (1:6, 10; 2:1-5; 3:1-5, 8-11, 14); rhizoids occurring scattered indiscriminately over the postical stem surface;[13] plants often with 1-2-celled gemmae (6:8-12) produced in fascicles (never with flat, discoid, solitary "gemmae"), rarely with caducous leaves; branches intercalary (2:1, 4), or if terminal, of the *Frullania*-type (2:1, 2, 5, 7-8). Suborder JUNGERMANNINAE, in large part).....12

12. Leaves complicate-bilobed (3:8-9, 11, 14, 14a), with a more or less sharp keel between the lobes (3:14k), the dorsal lobe smaller than the ventral, lying usually loosely over the ventral; leaf margins usually denticulate (3:8-9, 11, 14); perianth moderately to very strongly dorsoventrally flattened, more or less open at mouth; no underleaves (3:13); inflorescence terminal; branching only intercalary and axillary; 1-2(3-4)-celled fasciculate gemmae usually abundant (6:12).
SCAPANIACEAE[26] (*Diplophyllum, Douinia, Macrodiplophyllum, Scapania*)

12. Leaves various, but never complicate-carinate: never with a small dorsal lobe folded over a larger ventral lobe (1:3, 6, 10; 2:1-5, 7-8); perianths not (or very slightly) dorsoventrally compressed (1:3-4, 10-11); underleaves varying from very large (2:7; 3:5) to absent (2:4; 3:3); leaf margins lacking fine denticulations (except sometimes in *Plagiochila*, 2:5).....13

13. Plants with rhizoids restricted to the bases of the underleaves, or to a cushioned, specialized area below them, usually occurring in distinct fascicles (5:6-7); anisophyllous, the underleaves *ca.* 0.05-0.4 the area of the leaves, but present throughout (5:6-7).....14

14. Leaves ovate or orbicular to quadrate, approximate to imbricate, persistent (1:10; 5:6); plants large (0.6-5 mm. wide), with ± distinctly succubously inserted leaves; (asexual reproduction, when present, by gemmae, 6:9-10).....15

15. Rhizoids confined to a small area at the base of the underleaves (5:6-7), the postical side of stem not forming cushioned, purplish-pigmented areas; capsule ovoid, with short, straight, valves (5:7); capsule wall with cells bearing distinct localized thickenings, in part semiannular.....16

16. Underleaves large, bilobed, often with 1-several marginal cilia; leaves alternate to subopposite, but not united at their dorsal bases (1:10); perianth well developed (1:10) not subtended by a perigynium; capsule wall 4-5-stratose; spore-elater ratio 1.5-2:1; gemmae, where present, from the leaf margins.
.....LOPHOCOLEACEAE (*Lophocolea, Chiloscyphus*)

16. Underleaves small (5:6-7), linear-lanceolate to subulate, entire; leaves opposite and usually slightly united at their dorsal bases, entire, margined; perianth reduced, laterally compressed, a bilabiate cylinder, subtended by a perigynium (5:7); capsule wall 2-stratose; spore-elater ratio 1:1; gemmae from the middle of the abaxial leaf faces.....SOUTHBYACEAE (*Arnellia*)

15. Rhizoids arising from, or from margins of, large cushioned purplish areas lying below the bifid underleaves; leaves entire, alternate; perianth short, subtended by a fleshy perigynium lying at an angle

to the stem; capsule cylindrical, with linear, spirally twisted, 2-stratose valves lacking localized thickenings; spore-elater ratio 1:1. ..... GYROTHYRACEAE (*Gyrothyra*)[14]

14. Leaves obcuneate to obdeltoid, distant, alternate, subtransversely oriented and inserted, freely caducous; plants minute (to 0.5 mm. wide), invariably sterile; gemmae absent..... ..... PLAGIOCHILACEAE, in part (*Anomylia*)[15]

13. Plants with rhizoids scattered (3:5; 5:2), usually over the entire postical stem surface (absent usually in *Herberta*);[16] leaves always clearly alternate (2:5, 8)..... 17

17. Leaves 2-several-lobed (2:1-2; 3:1-4) or with leaf-margins clearly dentate or denticulate (1:6; 2:5)..... 18

18. Underleaves very large: either bilobed (2:7) and similar to leaves in size and form or (*Pleuroclada*) ovate-lanceolate and entire; leaves virtually transversely inserted and oriented, uniformly bilobed (2:7-8); without any form of specialized asexual reproduction (rarely with regenerations); perianths terminal on main stem; antheridial stalk biseriate. 19

19. Leaves bifid 1/2-4/5, somewhat secund, with slightly to distinctly falcate lobes, each provided with a "vein" of elongated cells; cells with bulging trigones; large oil bodies present, numerous, ± homogeneous; underleaves as large as leaves, but not secund; androecia with antheridia in bracteoles as well as in bracts; capsule wall 5-7-stratose; branches only intercalary and axillary. ..... HERBERTACEAE (*Herberta*)

19. Leaves bilobed to bifid, symmetrical, the lobes straight (2:7-8), consisting of uniform cells, the cells thin to equally thick-walled; oil bodies absent or minute; underleaves various; androecia with antheridia absent from bracteoles; capsule wall 2(-3)-stratose; branches lateral and of the *Frullania*-type, terminal (2:7-8). ..... HYGROBIELLACEAE[17] (*Hygrobiella, Pleuroclada, Anthelia*)

18. Underleaves small (if conspicuous, bifid and pluriciliate; 3:5) or absent (2:4; 3:3, 7); leaves never "veined."..... 20

20. Plants minute, usually 3-10 mm. long, typically with distant, nearly or quite transverse leaves (2:2); leaves bilobed 1/3-3/4, the lobes only 3-9 cells wide at base (2:2); often with small underleaves; cells small, at bases of lobes only 9-15 (rarely 16-18) μ wide; sporophyte with seta of 4 epidermal and 4 inner rows of cells (7:10). ..... CEPHALOZIELLACEAE (*Cephaloziella*)[18]

20. Plants larger, usually 8-80 mm. long, with leaves succubous (2:2-5) or transverse (3:2), usually approximate to imbricate; leaves variously lobed or dentate, but the chief lobes always more than 9 cells wide at base; leaf-cells usually 18-25 μ wide or more; sporophyte with seta of 8-many epidermal and many inner rows of cells (7:1-4, 8-9). 21

21. Leaf margins more or less denticulate (1:6) or dentate 2:5), often spinose-dentate, or bearing coarse teeth or lobes; leaves never regularly 2-4-lobed with entire lobes, often with asexual reproduction by propagula (broodbodies) on the leaf surface or by caducous

leaves or leaf lobes; dorsal leaf base with margin ± strongly reflexed (2:5); perianth terminal, laterally compressed (1:6). ..... PLAGIOCHILACEAE in part (*Plagiochila*)[19]

21. Leaves regularly 2-4-lobed, the lobes not normally dentate (2:2; 3:1-5); asexual reproduction (when present) by gemmae (6:8-12), never by caducous leaves or lobes or propagula; dorsal leaf margin flat or incurved (2:2,3; 3:1-2, 4), never forming a reflexed fold; perianths (1:3-4, 7pt) never laterally compressed, sometimes lacerating. 22

22. Female inflorescences (and perianth or perigynium) on more or less short *ventral* branches; androecia usually on short (rarely elongate) ventral branches; leaves 2-lobed, usually very obliquely inserted (except *Nowellia*); spore-elater ratio 1:1; capsule wall 2-stratose; antheridial stalk 2-seriate 23

23. Distinct large underleaves present; perigynium present (with perianth either at summit of perigynium or absent); with distinct oil bodies, 4-5 μ long or more; stem without a hyaloderm, the cortical cells small, opaque; leaf cells thin-walled, with small to discrete trigones; seta of numerous rows of subequal cells. ..... HARPANTHACEAE (*Harpanthus, Geocalyx*)

23. Underleaves absent or vestigial and occasional; perigynium absent; a distinct, elongate, trigonous perianth present; oil bodies absent or very minute; stem usually with a hyaloderm, the cortical cells large, pellucid; leaf cells non-collenchymatous: the walls thin or equally thickened; seta (at least when young) of 4 inner and 8 epidermal cell-rows. ..... CEPHALOZIACEAE (*Cephalozia, Nowellia, Cladopodiella*)

22. Female inflorescences terminal on main (1:3; 5:1-8) or lateral shoots; male inflorescences terminal (or becoming intercalary) on main shoots; branching lateral (2:2-3); leaves 2-5-lobed (3:1-5); spore-elater ratio *ca.* 2:1. 24

24. Perianth well developed, elongate, projecting beyond bracts, usually without a subtending perigynium (1:3-4); leaves 2-5-lobed for 1/6-3/4 their length, succubous or transverse (2:2; 3:1-5); cells of leaf lobes mostly 15-45 μ; leaf cells usually with 5-30(35-50) oil bodies per cell; plants sometimes with minute to rather large underleaves (3:5); normally with some form of asexual reproduction (6:11) 25

25. Perianth terete, more or less contracted to the mouth, clearly widest below mouth (1:4); usually with some type of asexual reproduction (fasciculate gemmae, rarely caducous perianths) (6:11); spores delicately verruculose; elaters completely 2-spiral; leaves 2-5-lobed 3:1-5) ..... LOPHOZIACEAE[20] (*Lophozia, Chandonanthus, Gymnocolea, Anastrepta, Acrobolbus, Saccobasis, Eremonotus, Anastrophyllum, Tritomaria, Mesoptychia*)

25. Perianth campanulate, widest at the open, truncate mouth, obtusely 4-plicate near mouth (1:3); with asexual reproduction by caducous perianths; spores delicately areolate; elaters 1- or partially 2-spiral, usually with spiral reduced in part to annulations; leaves simply 2-lobed (1:3); capsule wall 2-stratose; seta of 8 outer, 4 inner cell-rows (7:9); leaf cells non-collenchymatous, very delicate. ..... CHONECOLEACEAE (*Chonecolea*)[21]

24. Perianth absent (5:8) or reduced (1:7 pt; 5:3-5) to a short tube (included within the bracts); leaves uniformly 2-lobed, usually for less than 1/3 their length (5:4-5), the lobes often obtuse or rounded; cells with mostly 2-5(6-12) large, prominent oil bodies; perigynium often present and well developed (5:4-5); without asexual reproduction; capsule wall 2-(rarely 3-)stratose.....26

26. Leaves strongly succubous (5:5); large, lanceolate underleaves present (5:5); cells of leaf lobes 25-36 μ.
.....JUNGERMANNIACEAE (*Nardia*, in part)[22]

26. Leaves essentially transverse (5:4); underleaves almost or entirely absent; cells of leaf lobes mostly 8-17 μ.
.....MARSUPELLACEAE (*Marsupella, Prasanthus, Gymnomitrium*)[23]

17. Leaves (at least on sterile portions of plants) entire, at most occasionally retuse at the apex (1:10; 5:5; 6:9); underleaves small, minute or absent (5:2), the plants very strongly dorsoventral; cells collenchymatous; trigones small to bulging, but intervening walls thin.....27

27. Plant with free development of postical stolons; branches entirely or partially postical in origin; perianths on short postical shoots, trigonous-prismatic; minute to small underleaves present, abundantly bearing slime-papillae; cells usually with large trigones, each cell with 2-4(5) very large, papillose oil bodies; sporophyte with capsule wall 2-stratose; seta of 8 epidermal, 4 interior cell-rows (7:9).
.....ODONTOSCHISMACEAE (*Odontoschisma*)

27. Plant without ventral stolons; branches all lateral; perianths terminal, terete or laterally compressed (1:6), never trigonous; underleaves absent, if present not margined with slime-papillae; seta with numerous cell rows (7:2-4).....28

28. Perianths strongly *laterally* compressed, bilabiate, wide at mouth (1:6); capsule wall 4-7-stratose; sterile shoots usually with small, lanceolate, or multifid or ciliate underleaves; cells with oil bodies either coarsely segmented or homogeneous; usually with some means of asexual reproduction; perigynium uniformly lacking.
.....PLAGIOCHILACEAE[24] (*Mylia, Plagiochila*)

28. Perianths terete or barely *dorsoventrally* compressed, usually narrowed (1:4) to a conical or beaked mouth; capsule wall 2-(rarely 3-4-) stratose; sterile shoots with underleaves absent or vestigial (except *Nardia*); no gemmae or other asexual means of reproduction (except *Jungermannia*); often with a distinct perigynium (5:3, 5).
.....JUNGERMANNIACEAE (*Nardia*, in part, *Solenostoma, Jamesoniella, Jungermannia, Cryptocolea*)[25]

III. Artificial Keys to Genera of Jungermanniales

The leafy liverworts so often occur only as persistently sterile forms that determination by means of the preceding key to families is often impossible. Furthermore, convergent evolution often makes it difficult if not impossible for a sharp separation of families. As a consequence, direct keys to genera are almost a necessity, particularly to those taxa that reproduce only vegetatively. Plants which reproduce only by specialized asexual means (gemmae, 6:8-12; broodbodies, 6:14; propagula, caducous leaves, perianths or branches, 6:13, etc.; see Degenkolbe, 1938) are often persistently sterile and often very difficult to place in the correct family or genus.[27] Such plants can hardly be identified even by an artificial generic key of the usual sort.

For these plants I have substituted a key based predominantly on the nature of the asexual reproduction. However, since the ability to reproduce asexually is not always realized, the second key to genera includes all genera from the area.

Plants with some mode of asexual reproduction (and usually without sex organs or sporophytes).[28] ..... KEY A

Plants without any obvious mode of asexual reproduction ..... KEY B

A. KEY TO ASEXUALLY REPRODUCING PLANTS[29]

1. Reproduction by caducous, juvenile or rudimentary branches bearing modified leaves and produced either from surfaces of persistent leaves or from stems (6:13). (Plants of this type with the "propagula" or "caducous shoots" producing only rudimentary leaves; when very young often recognizable as mere clumps of cells arising from leaf surfaces; in the latter case beware of possible confusion with discoid gemmae) 2

1. Asexual reproduction not involving caducous branches or shoots; the leaves never developing clumps of cells from their surfaces that mature into leafy shoots 6

2. Caducous shoots ("propagula") produced on the leaf-surfaces, often in large numbers, at times superficially like regenerations from the leaves. 3

2. Caducous shoots in the form of small lateral branches with only 1-2 pairs of leaves on abscission (6:13); underleaves with slender, divaricate lobes. 5

3. Leaves succubous, ± dentate (2:5); underleaves minute, formed of cilia or laciniae ..... *Plagiochila*[30]

3. Leaves incubously inserted and complicate-bilobed, the large dorsal lobe entire (2:9); underleaves large, bilobed or entire (2:9) 4

4. Underleaves bilobed; predominantly red-brown plants ..... *Frullania*

4. Underleaves entire (4:14); green to olive plants ..... *Porella*

5. Leaves acute to acuminate (6:13) ..... *Drepanolejeunea*

5. Leaves elliptical, rounded or blunt ..... *Leptolejeunea (elliptica)*

6. Reproduction by caducous or fragmenting leaves 7

6. Reproduction never by caducous or fragmenting leaves 18

7. Leaves caducous at the very base, the whole leaf caducous (except, in some cases the lobule of a complicate-bilobed leaf) 8

7. Leaves irregularly fragmenting, only the distal portion of the leaf breaking free along irregular schizolytic lines, leaving an irregular leaf base. ..... *Plagiochila*[30] *(caduciloba, yokogurensis)*

8. Leaves succubously shingled or transverse; underleaves very small or lacking 9

8. Leaves incubous or incubous-complicate (then with the larger dorsal lobe entire) 11

9. Leaves remote and small, nearly transverse, obcuneate to obdeltoid; with distinct lanceolate underleaves; rhizoids only at underleaf bases; plant minute ..... *Anomylia (cuneifolia)*[31]

9. Leaves quite oblique, succubous, not narrowed to base; underleaves minute or absent; rhizoids scattered or lacking 10

10. Leaves ± dentate, without marginal rhizoids; cuticle smooth. ..... *Plagiochila*[32]

10. Leaves bilobed, with occasional to numerous marginal rhizoids; cuticle closely verrucose..... *Acrobolbus* (*ciliatus*)[33]

11. Leaves unlobed, simply incubous, the apex usually 2-3-dentate; postical flagella with reduced leaves present. ..... *Bazzania* (*denudata, nudicaulis*)

11. Leaves incubous-complicate (the small ventral lobe bent under the large dorsal lobe); no stolons or flagella present.....12

12. Caducous leaves only on erect or ascending, worm-like branches with short internodes and persistent underleaves; the caducous leaves small, modified in shape.....13

12. Caducous leaves on normal, unmodified shoots, with normal internodes, the branches not erect.....15

13. Underleaves entire..... *Ptychocoleus* (*heterophyllus*)[34]

13. Underleaves bilobed 14

14. Reddish-brown; northern; lobules helmet-shaped, parallel with stem. ..... *Frullania* (*bolanderi*)

14. Green; subtropical or tropical; lobules inflated, parallel with posterior leaf margin..... *Rectolejeunea* (*berteroana*)

15. Underleaves lacking (2:6)..... *Radula*

15. Underleaves very large.....16

16. Plants reddish-brown; lobules parallel with stem. ..... *Frullania* (*choracensis*)[35]

16. Plants greenish; lobules lying parallel with posterior margin of lobe. 17

17. Olive to deep green, firm; lobules with a hyaline papilla lying in sinus *distal* to the apical tooth..... *Cheilolejeunea* (cf. *polyantha*)[36]

17. Pale to yellow-green, delicate; lobules, where inflated, with hyaline papilla at base of apical toothe, just toward stem from apical tooth. ..... *Rectolejeunea*

18. Asexual reproduction by "gemmae" or "brood-bodies" of some type, arising from the apices (and/or surfaces) of the leaves (6:4-5, 8-12). 19

18. Asexual reproduction by caducous perianths; plants with succubous, bilobed leaves (1:3; 2:2-4); without or with minute underleaves; cells without trigones. 57

19. "Gemmae," many-celled flat bodies (= "broodbodies"), arising singly from the margins or surfaces of the leaves (6:14); leaves incubous-complicate (4:5, 7-10, 13).....20

19. Gemmae of 1-2, rarely 3-5 cells, never forming flat plates (6:8-12); leaves not incubous-complicate (1:10; 2:1; 3:1-5, 14).....25

20. Underleaves absent (2:6).....21

20. Underleaves large, conspicuous.....24

21. Plants small or minute, 400-850 μ wide; leaves usually narrowed or pointed toward apex; rhizoids arising from stem; gemmae not attached to leaf by a marginal cell of the gemma.....22

21. Plants relatively large: 750-2500 μ wide; leaves ovate or subrotund

(2:6); rhizoids only on lobules (2:6); gemmae from leaf margins, attached by marginal cells of gemmae.....*Radula*

22. Gemmae usually arising on the leaf surfaces (sometimes occasional gemmae marginally attached); lobules near apex with 2 teeth separated by a broad sinus; leaves rarely dimorphic.....23

22. Gemmae arising only from marginal cells of leaves; lobules appearing to bear a single apical tooth; plants minute, hyaline; leaves sharply dimorphic.....*Aphanolejeunea*[37] (*cornutissima, ephemeroides*)

23. Leaves not tipped by hyaline cells.....*Cololejeunea*[38]

23. Leaves of mature shoots with a cluster of hyaline, finger-like cells at apex .....*Leptocolea* (*cardiocarpa*)[39]

24. Underleaves entire or slightly emarginate. .....*Caudalejeunea* (*lehmanniana*)

24. Underleaves with obvious, divaricate lobes. .....*Diplasiolejeunea* (*rudolphiana*)[40]

25. Leaves simply incubous, entire or minutely bidentate at apex; underleaves large, rhizoids confined to their bases.....*Calypogeia*[41]

25. Leaves succubous, transverse, or succubously complicate-bilobed (2:1-5, 7-8); 3:1-5). 26

26. Leaves entire (5:6), their margins never dentate.....27

26. Leaves variously lobed, toothed or complicate-bilobed (3:1-5, 14).....33

27. Leaves opposite; gemmae from middle of abaxial leaf surfaces (6:9-10). .....*Arnellia* (*fennica*)[42]

27. Leaves clearly alternate; gemmae otherwise in origin.....28

28. Gemmae in large part 2-several celled (6:10-12).....29

28. Gemmae uniformly 1-celled.....32

29. Gemmae from the tips of ± erect, attenuated shoots with reduced leaves; cells under 30 μ in leaf middle; underleaves absent, or copiously provided with slime papillae.....30

29. Gemmae arising from margins of more or less normal-sized leaves, not from attenuate, erect shoots; underleaves distinct, without slime papillae. 31

30. Postical stolons present; leaves orbicular; oil bodies (1)2-4(5) per cell, very large; branches partly or entirely postical.....*Odontoschisma*

30. Stolons absent; leaves oblong; oil bodies numerous, small; branches exclusively lateral.....*Jungermannia* (*lanceolata*)

31. Underleaves lanceolate; rhizoids dense, numerous, scattered; cells coarse and large, with coarse trigones.....*Mylia* (*anomala, taylori*)[43]

31. Underleaves various, partly bilobed; rhizoids few, only at base of underleaves; cells delicate, without trigones.....*Chiloscyphus* (*gemmiparus*)

32. Gemmae arising from slender shoots, external in origin; underleaves large; leaves ovate to elliptic.....*Gyrothyra* (*underwoodiana*)[44]

32. Gemmae arising internally from swollen shoot tips; underleaves absent; leaves rotundate.....*Solenostoma* (*caespiticium*)

33. Leaves simply 2-several-lobed; never finely denticulate (3:1-5).....34

33. Leaves complicate-bilobed, the lobes usually denticulate (3:8-9, 11).....55

34. Mature leaves mostly 3-4-lobed (3:4-5).....35

34. Mature leaves nearly uniformly bilobed (3:1, 2).....39

35. Leaves 3-4-lobed to base, the filiform lobes uniseriate; gemmae produced uniseriately from lobe apices, spherical, 1-celled (6:4-5). ..... *Blepharostoma* (*trichophyllum*)[45]

35. Leaves 3-4-lobed to middle or less, the lobes broad (3:4-5); gemmae originating from apices of branched fascicles (6:12), 2-celled when mature. 36

36. Leaves obliquely inserted; usually with at least minute underleaves (3:4-5). 37

36. Dorsal half of leaves transversely inserted and ± transversely oriented; underleaves absent (3:2-3) 38

37. Leaf lobes, or some of them, sharply cuspidate; postical leaf bases with 1-several long cilia formed of elongated cells. ..... *Lophozia* subg. Barbilophozia[46] (*hatcheri, lycopodioides*)

37. Leaf lobes blunt to acute, never cuspidate; postical leaf bases without long cilia formed of elongated cells (3:4-5). ..... *Lophozia* subg. Orthocaulis[47]

38. Cortical cells 1.5-4:1; dorsal half of insertion of leaf transverse; leaf lobes usually sharp ..... *Tritomaria*[48]

38. Cortical cells 4-8:1; dorsal half of insertion of leaf arched towards stem apex leaf lobes usually blunt ..... *Saccobasis* (*polita*)[49]

39. Rhizoids only at underleaf bases; underleaves bifid, each lobe usually with 1-2 marginal teeth; gemmae greenish or yellow, irregular, often forming 3-5-celled clumps (6:8) ..... *Lophocolea* (*heterophylla, minor*)

39. Rhizoids scattered over postical stem face (3:10); gemmae regularly 1-2-celled, often angulate (6:11) 40

40. Underleaves large, united on one side with stem leaves. ..... *Harpanthus* (*scutatus*)

40. Underleaves minute or absent, if present free from leaves 41

41. Gemmae smooth, without sharp angles, ovoid or spherical to elliptical (6:12). 42

41. Gemmae, at least in part, pyriform to stellate or polyangulate (6:11) ... 46

42. Leaves clearly transversely oriented (2:1); cells ± equally thick-walled. 43

42. Leaves quite obliquely to nearly horizontally inserted and oriented ... 44

43. Leaf lobes running out into slender cilia; leaf bases inflated, gibbose. ..... *Nowellia* (*curvifolia*)

43. Leaf lobes acute or blunt (2:1); leaf bases flat or weakly concave. ..... *Cephaloziella* subg. Cephaloziella[50]

44. Underleaves distinct, if small; cells with coarse trigones; cuticle verrucose ..... *Lophozia* subg. Leiocolea (*heterocolpa*)[51]

44. Underleaves absent; cells thin- to ± thick-walled; cuticle smooth 45

45. Stem with cortex of large, pellucid cells; no oil bodies; leaves with sharp, often connivent lobes ..... *Cephalozia*

45. Stem with cortex of small, opaque cells; with oil bodies; leaves with divergent, variable, often blunt lobes ..... *Lophozia* subg. Massula[52]

46. Leaves transversely inserted and oriented (3:2-3) 47

46. Leaves obliquely inserted and oriented (2:2-4) 50

47. Leaves ± dentate; southwestern only.
.....*Cephaloziella* subg. Prionolobus (*turneri*)

47. Leaves with lobes entire (except with gemmae formation) (3:2-3); widespread. 48

48. Plants small or minute: less than 1 mm. wide; dorsal leaf base not decurrent (3:2); cells ± thick-walled.....49

48. Plants larger: 0.8-2 mm. wide; dorsal leaf-base short-decurrent (3:1); cells with large trigones.
.....*Anastrophyllum* subg. Anastrophyllum (*michauxii*)

49. Gemmae all 1-celled, vineous, only 10-11 μ, on exceedingly slender, abnormal shoots with erect, reduced, appressed leaves.
.....*Eremonotus* subg. Crossocalyx (*hellerianus*)[53]

49. Gemmae partly 2(-3)-celled, yellow-red to scarlet, larger; gemmae on ± reduced stems, but never on filiform shoots with vestigial leaves.
.....*Eremonotus* subg. Sphenolobus (*minutus*)[54]

50. Posterior leaf margin strongly reflexed; leaves very shallowly emarginate; North Pacific coast only.....*Anastrepta* (*orcadensis*)

50. Posterior leaf-margin not reflexed; leaves distinctly bilobed; widespread. 51

51. Stem with small, opaque cortical cells; leaves without sharply connivent lobes with oil bodies.....51

51. Stem with large, hyaline cortical cells; leaves with connivent lobes; no oil bodies.....*Cephalozia* (*media*)

52. Postical stolons present; underleaves distinct (cells only 17-23 μ, strongly thick-walled; leaves only 1/5-1/6-bilobed, with a very narrow sinus; only in Northeast).....*Cladopodiella* (*francisci*)

52. Stolons and underleaves absent.....53

53. Cell walls strongly but ± equally thickened; gemmae orange-red.
.....*Lophozia* subg. Isopaches (*bicrenata*)[55]

53. Cell walls thin or with trigones distinct.....54

54. Cells ± collenchymatous; gemmae greenish or reddish; stem with medulla strongly mycorrhizal ventrally, the mycorrhizal cells small in diameter and brownish with age.....*Lophozia* subg. Lophozia[56]

54. Cell walls usually thin or slightly and evenly thickened; gemmae greenish, sharply stellate; stem with medullary cells uniform, without ventral mycorrhizal small-celled band.
.....*Lophozia* subg. Massula (*grandirctis, obtusa, incisa*)[57]

55. Gemmae smooth, ovoid to subspherical or ellipsoid, 1-2-celled 6:12).
..... *Scapania*[58]

55. Gemmae polygonal to stellate (6:11).....56

56. Gemmae 1-2-celled; small plants whose marginal leaf cells are equally thick-walled; widespread .....*Diplophyllum*

56. Gemmae (2)3-4-celled; large plants, whose marginal cells are thin-walled but provided with large trigones; northwest Pacific.
..... *Macrodiplophyllum*[59]

57. Perianth subspherical to ovoid, contracted to mouth; northern; sun forms blackish. .....*Gymnocolea*

57. Perianth campanulate, broad at the mouth (1:3); tropical; only on palm trunks; sun forms violet.....*Choneolea*[60]

B. KEY TO PLANTS NOT OBVIOUSLY REPRODUCING ASEXUALLY

1. Leaves divided for 0.6-0.9 their length into filiform segments 1-2 cells broad, or into cilia (6:5), or deeply lobed, the lobes fringed with long, uniseriate cilia (4:1, 3), *the leaf thus largely resolved into uniseriate segments.* 2

1. Leaves entire or lobed, but *with greater part of lamina evident* (2:1-8), if lobed, the lobes not freely ciliate, the cilia not 1-2 seriate (3:1-5, 11, 14). 6

Leaves with lamina largely resolved into cilia or filiform lobes; rhizoids (when present) confined to the bases of the large underleaves (couplets 2-5).

2. Plants robust; leaves lobed to the middle or beyond, the lobes ciliate; leaves incubously shingled (4:1, 3) or succubous; underleaves large, pluriciliate, usually with rhizoids at base..... 3

2. Plants minute, filiform and slender, less than 0.6 mm. wide; leaves transverse or subtransverse, divided virtually to base into (2)3-4 slender segments only 1-2(3) cells wide at base (6:4-5); underleaves of 2-3 filiform segments 1 cell wide to base, with rhizoids..... 4

3. Plants whitish-green; lamina resolved largely into narrow lobes fringed with very numerous, branched cilia; cuticle verruculose; leaves succubously inserted; cells without trigones..... *Trichocolea*

3. Plants green to fulvous to reddish-brown; lamina obvious, the rather broad lobes fringed with simple cilia (4:1, 3); cuticle smooth; leaves incubously inserted and shingled; cells with bulging trigones..... *Ptilidium*

4. Leaf segments formed of delicate, elongate (50-100 μ) cells that ± collapse on drying; cuticle smooth; stem with hyalodermis; underleaves of 2(3) very short divisions; *shiny when dry*..... *Telaranea*[61]

4. Leaf-segments formed of short, rigid cells (under 50 μ long) that do not collapse in drying (6:4-5); cuticle usually delicately verruculose; stem without a conspicuous hyalodermis; *dull when dry*..... 5

5. Underleaves reduced to 2-3 very short divisions; leaves with lobes 2(3-4) cells wide at base; plants regularly pinnately branched; sun forms brownish-tinged. ..... *Microlepidozia*[62]

5. Underleaves similar to leaves, of 3-4 filiform segments; leaves with lobes uniseriate to base (6:4-5); plants irregularly monopodially branched; yellow-green in sun..... *Blepharostoma*

6. Leaves (or all but their postical base) obviously incubously inserted and shingled; *the plant in antical view with the dorsal leaf margin lying nearer the stem apex than the postical leaf margin* (4:5, 13); stem with rhizoids always restricted in origin: either at bases of some underleaves (4:11, 12) or from lobules of some leaves (2:6)..... 7

6. Leaves transverse (2:1, 8; 3:2) or succubously inserted (2:3, 5): *the plant in antical view with leaves evidently transversely oriented, or with the dorsal margin lying nearer base of stem than the postical leaf margin* (3:4); (in *Diplophyllum* and *Scapania*, *i.e.*, the Scapaniaceae, the leaves succubous-complicate, the larger postical lobe succubously inserted and shingled, but the smaller antical lobe incubously oriented [3:9,14]). 35

7. Leaves not complicate-bilobed, without an incurved small postical fold or

lobe (lobule); sexual branches postical in origin; underleaves large and obvious 8

7. Leaves complicate-bilobed, with the smaller postical "lobe" (lobule) folded under the larger antical "lobe" (2:6, 9), thus hidden in antical aspect (4:5, 13); lobule rarely reduced to a minute basal fold; sexual and all other branches lateral in origin (2:6; 4:14); underleaves sometimes absent (2:6). 10

Leaves simply incubous, without postical lobule; rhizoids restricted to underleaf bases; underleaves very large (couplets 8-9).

8. Leaves divided to the middle into 3-4 lobes; underleaves similarly 3(4)-lobed; branches often running out into flagella; branches loosely pinnate; without postical flagella..... *Lepidozia*

8. Leaves entire or 2-3-dentate at the very apex; underleaves entire, bilobed, or irregularly dentate; leafy branches never running out into flagella. 9

9. Leaves usually 2-3-dentate at the apex; stems freely producing postical flagella; plants firm, opaque, green to brownish, without gemmae, but sometimes with caducous leaves; plants terminally, pseudodichotomously furcate. ..... *Bazzania*

9. Leaves entire or minutely bidentate at apex; stems without slender, postical flagella; plants delicate, pellucid, pale to bluish- or greyish-green, often with gemmae; plants usually with simple shoots, developing postical, intercalary branches. ..... *Calypogeia*

Leaves complicate-bilobed and incubous, with postical lobule; branches all lateral; without stolons or flagella; without 1-2-celled gemmae; perianths commonly produced; without perigynia. (couplets 10-34).

10. Underleaves absent (2:6); leaves often with discoid, many-celled gemmae (6:14). 11

10. Underleaves present, bilobed (2:9) or entire (4:14); without discoid gemmae (except in *Caudalejeunea* and *Diplasiolejeunea*)..... 14

11. Rhizoids on stem; minute or small, pellucid or yellow-green plants, less than 800 μ wide; leaves usually acute or subacute at apex; lobes and lobules very narrowly attached to stem..... 12

11. Rhizoids originating on (some) postical lobes, not on the stem (2:6) medium-sized, firm, opaque plants, usually 850-1500 μ wide; leaves subrotund, broadly rounded at apex (4:4-5); lobes and lobules broadly united with stem (4:7-9)..... *Radula*

12. Leaf apices without hyaline cells; perianth not compressed..... 13

12. Some leaf apices with clusters of hyaline, finger-like cells; perianth compressed. ..... *Leptocolea*[63]

13. Exceptionally delicate, minute, and pellucid plants; lobules often largely vestigal; inflated lobules with apex formed of 2 juxtaposed teeth, separated by a slight, narrow sinus; gemmae only from marginal cells of lobe. ..... *Aphanolejeunea*[64]

13. Small to minute plants; inflated lobules with apex formed of 2 teeth (one of which is actually in the sinus between keel and lobule apex), the 2

teeth widely separated by an open, broad sinus; gemmae never confined to marginal cells of lobe.....*Cololejeunea*[65]

14. Underleaves unlobed or obscurely notched (but sometimes ciliate) (4:14).....15

14. Underleaves obviously bilobed (2:9; 6:13).....23

15. Lobule lingulate or oblong, lying parallel with stem, almost free from stem (keel very short or obsolete) (4:13-14); very coarse plants, 2.5-5 mm. wide.....16

15. Lobule inflated, lying parallel with posterior leaf margin, attached to it by a long keel (1:12); minute or small plants (0.25-2.5 mm. wide usually).....17[66]

16. Leaves without water sacs (or entire lobule inflated to form a ± distinct water sac); underleaves without water sacs (4:12, 14); cells smooth, not elevated as prominent papillae; leaves and underleaves in our species, not longly ciliate on margins; 4:13, 14; plants green to olive-green.....*Porella*[67]

16. Leaves, both at base of lobe and at base of lobule, with a small portion of the basal margin inflexed to form a sharply defined water sac; underleaves at base, on each side, similarly involute to form water sacs; cells of leaves elevated to form ± truncate, prominent papillae; leaf and underleaf margins prominently ciliate; plants blackish.....*Ascidiota*[67]

17. Margin of lobule with 4-6 minute teeth; perianth pluriplicate (1:12)...18

17. Margin of lobule with 1(2) teeth at or near apex, or quite entire; perianth with only 3-5 blunt or sharp carinae.....19

18. Plants with erect, worm-like shoots (denuded of leaves); plants golden to pale brownish, usually sterile; cells with numerous nodular intermediate thickenings.....*Ptychocolcus*[68]

18. Plants without erect, caducous-leaved shoots; mature shoots fuscous to blackish-green, always fertile (1:12); cells virtually without intermediate thickenings.....*Brachiolejeunea*

19. Plants greyish-green to green, or olive-green, without fuscous pigmentation.....20

19. Plants fuscous to blackish-green in color, the cell walls pigmented.....21

20. Underleaves shallowly notched; plants, with maturity, producing erect or ascending shoots; each cell with many minute, homogeneous oil bodies; perianth sharply trigonous.....*Caudalejeunea*

20. Underleaves reniform to orbicular, broadly rounded distally; plants closely appressed to substrate; each cell with a large, compound oil body; perianth (4)5-carinate.....*Leucolejeunea*

21. Lobules at apex with a sharp, long, curved apical tooth; lobule strongly inflated, its anterior margin involute throughout its length; underleaves clearly distant.....*Neurolejeunea*[69]

21. Lobules at apex with an obscure apical tooth, or without a perceptible one; lobules inflated largely near base and along keel, the free, anterior margin flatly pressed against lobe, visible without flattening leaf; underleaves usually approximate to imbricate.....22

22. Plants closely appressed to substrate, shiny and flat when dry; underleaves rotund-reniform, clearly wider than long; cells with numerous

minute oil bodies; perianth with 4 dentate keels hardly emergent from beyond bracts.....*Lopholejeunea*

22. Plants with maturity ascending or suberect, dull; leaves convolute when dry; underleaves obdeltoid, subtruncate distally; cells with 2-4 large, segmented oil bodies; perianth with 3 smooth keels, longly emergent from beyond bracts.....*Mastigolejeunea*

23. Lobule always conspicuous, attached by a very narrow, stalk-like base, appearing free from the stem; lobule helmet-shaped, usually lying nearly parallel with stem (in some cases explanate, then clearly parallel with stem); plants opaque, deep green to reddish-brown; underleaves inserted on over 4 rows of stem cells.....24

23. Lobule distinctly and usually broadly attached to stem (or else obsolete); plants usually pale to yellow-green, but sometimes olive to reddish-brown; underleaves attached to only 2 rows of large ventral cortical cells.....25

24. Leaves rounded at apex (except in the copper-colored *F. tamarisci*); plants on drying not blackish; plants of dry rocks or bark; underleaf lobes blunt to acute.....*Frullania*

24. Leaves (at least when young) apiculate at apex; plants commonly black on drying; plants of wet, deeply shaded rocks; underleaf lobes usually acuminate.....*Jubula*

25. Underleaves widest near middle, with lobes nearly erect or connivent; dorsal lobes ovate-orbicular to oblong-ovate, less than 1.3 as long as wide.....26

25. Underleaves with lobes uniformly and sharply divergent (6:13), the underleaf thus widest at apex. (Prominent, glistening ocelli present.).....32

26. Lobule (on mature, lobulate leaves) with a slight notch *beyond* apical tooth (*i.e.*, in sinus between apical tooth and keel), in which notch is situated the hyaline papilla;[70] plants firm, olive- to dull whitish-green, opaque; cells more or less collenchymatous or thick-walled, each with 1-3(4) very large, coarsely segmented oil bodies.....*Cheilolejeunea*[71]

26. Lobule (on mature lobulate leaves)[72] with a slight notch at *proximal base* of apical tooth (*i.e.*, on side of apical tooth towards the stem); in this notch is situated the hyaline papilla (6:13);[73] cells in most cases with (3)4-10 or more smaller, finer-segmented, or homogeneous oil bodies which never nearly fill the cell lumen.....27

27. Plants brownish-tinged, shiny when dry (at times appearing merely bronzed or olive-green); cell walls with a prominent brownish middle lamella; leaves with (1)2-several large ocelli at base; apical tooth of lobule prominent but 1-celled, hooked.....*Ceratolejeunea*[74]

27. Plants various shades of green, never brown or bronzed; middle lamella inconspicuous under oil immersion; leaves usually without ocelli (in the minute plants of subg. Microlejeunea rarely with 1-2 basal ocelli); apical tooth usually small (if very elongate, formed of several cells).....28

28. Leaves always clearly persistent on the stem; perianths not strongly dorsoventrally compressed (except subg. Chaetolejeunea; this taxon with long, filiform apical tooth of the lobules).....29

28. Leaves (on at least some stems) clearly caducous; perianths strongly dorsoventrally compressed, often obcordate, the antical keel low or absent (1:8-9); lobules often partly vestigial, but never with linear, low

apical teeth. (Cells hexagonal and ± equally thick-walled, less than 20 μ.) ..... *Rectolejeunea*

29. Perianths with the 5 keels smooth or barely crenulate due to protuberant cells, contracted into a distinct beak; leaves always broadly rounded at apex, the margins entire to faintly crenulate (2:9); cells with usually vestigial to small (rarely pronounced) trigones, and without, or rarely with few intermediate thickenings..... 30

29. Perianths variously modified: in ours either with keels obsolete (and then without a beak) or with keels denticulate with 1-3-celled teeth; leaves at apex commonly apiculate (at least on juvenile leaves); cells with large trigones and numerous intermediate thickenings..... 31

30. Underleaves narrowed or rounded at base, bilobed with an open sinus, small to moderate in size: varying from remote and no wider than stem (2:9) to 2-3 × as wide as stem and then contiguous to subimbricate; gynoecia usually with 1 subfloral innovation, thus becoming pseudolateral (2:9); leaf lobes flat or weakly convex, never deflexed; plants minute to small (200-1500 μ wide), never flaccid. ..... *Lejeunea s. lato*[75]

30. Underleaves rounded to cordate at base, narrowly incised with a frequently closed sinus, very large: 3-7 × as wide as stem, imbricate; gynoecia usually with 2 subfloral innovations, and then situated in the fork of a dichotomy; leaf lobes convex, with the apices deflexed to involute; plants robust (1-2 mm. wide), but delicate and ± flaccid. ..... *Hygrolejeunea*[76]

31. Immature leaves always apiculate or mucronate; perianth with keels denticulate, contracted into a distinct beak; underleaves small, little wider than stem, narrowed to base..... *Crossotolejeunea*

31. Immature leaves usually obtuse to rounded at apex, but mature ones sometimes obtusely pointed, with sometimes a weak subapical tooth; perianth (in ours) with keels obsolete, smooth, the truncate perianth apex without a beak; underleaves large, 2-3 × as wide as stem, rounded or subcordate at base..... *Taxilejeunea*[75]

32. Dorsal lobes broadly rounded, broadly ovate-rotundate; underleaves as many as lateral leaves; lobules with a long, filiform tooth. ..... *Diplasiolejeunea*[77]

32. Dorsal lobes ovate-lanceolate and pointed (6:13) or narrowly elliptical; underleaves half as many as leaves; lobules with a small, 1-celled apical tooth (6:13)..... 33

33. Leaf lobes obtuse to rounded, the leaf elliptical in outline; underleaves with a sharp division into large, pellucid marginal cells and very small central, rhizoid-developing cells; living plant with strong odor of licorice. ..... *Leptolejeunea*

33. Leaves sharply acute to acuminate at the apex, ovate-lanceolate in outline, falcate (6:13); underleaves formed of essentially uniform, uniformly small cells; living plant odorless..... 34

34. Lobes of underleaves filiform, 1 cell wide (6:13)..... *Drepanolejeunea*

34. Lobes of underleaves blunt and broad, several cells wide. ..... *Harpalejeunea*

Leaves succubous or transverse (in Herberta, *which has vittate, bifid leaves, inserted slightly incubously, but transversely oriented or postically secund) (couplets* 35-88).

35. Leaves variously lobed, or at least their margins with distinct teeth (1:6; 2:1-8; 3:1-5, 14).....36

35. Leaves entire and unlobed (rarely isolated leaves weakly emarginate) (5:6); underleaves absent or considerably smaller than leaves (5:6)....76

36. Underleaves similar to, and as large (or virtually as large) as the leaves (2:7); leaves and underleaves both bilobed, both essentially transversely inserted (2:7-8).....37

36. Underleaves distinctly smaller than the leaves (and differing from them in dentition, and/or the number of lobes; 3:5; 5:5) or absent (3:3, 13); leaves (and underleaves, if present) 2-4-lobed.....39

Leaves and underleaves transverse, similar in size and shape; leaves bilobed; at least median leaf cells distinctly elongated (couplets 37-38).

37. Leaves divided to below the middle, the lobes sharply acute (2:7-8); rhizoids largely inserted on leaves or at underleaf bases.....38

37. Leaves shallowly bilobed, the lobes obtuse or subacute; rhizoids scattered on ventral side of stem.....*Hygrobiella*

38. Leaves vittate, the cells with coarse, bulging trigones; leaves spreading, ± secund, the lobes often falcate; branches few, all intercalary; rhizoids rare; Appalachian.....*Herberta*[78]

38. Leaves formed of uniform cells, the cells equally thick-walled, without trigones; leaves erect-appressed, not secund (2:7-8); branches frequent, lateral and terminal; rhizoids frequent; arctic and alpine.....*Anthelia*

39. Leaves distinctly complicate-bilobed, the smaller antical lobe bent over the larger postical lobe (3:9, 14), thus the shoot appearing to bear 4 rows of leaves; keel between dorsal and ventral lobes usually sharp (3:9a, 14k, 14a); underleaves lacking (3:13); (leaf margins usually finely denticulate).....40

39. Leaves not sharply complicate-bilobed (3:1-5, 2a).....43

Leaves complicate-bilobed, the antical lobe smaller than the postical; branching only lateral and intercalary; no underleaves. Scapaniaceae (couplets 40-42).

40. Leaf lobes ± acuminate, very gradually narrowed and lanceolate to acutely triangular; leaf cells with a waxy cuticle; gemmae absent; perianth plicate, hardly compressed, ciliate at mouth; elaters 1-spiral; western.[79].....*Douinia*

40. Leaf lobes abruptly narrowed or mucronate, or rounded, not lanceolate (3:8-9, 11, 14); leaf cells with papillae, or cuticle smooth, not suberized; gemmae usually present (6:12); elaters 2-spiral.....41

41. Gemmae smooth, ellipsoidal (6:12); leaf lobes rotund to reniform to ovate or short lingulate (3:11, 14); perianth sharply compressed, wide at mouth.....*Scapania*[80]

41. Gemmae sharply angulate-stellate; leaf lobes narrowly lingulate to oblong-lingulate (3:8-9); perianth little compressed, sharply plicate, narrowed to mouth.....42

42. Gemmae 1-*2*-celled; leaves not decurrent postically (*3*:8); small plants whose leaves bear 1-several marginal rows of thick-walled cells. ..... *Diplophyllum*

42. Gemmae (*2*)3-4-celled; leaves ± decurrent postically; robust plants whose leaves are formed of collenchymatous cells throughout. ..... *Macrodiplophyllum*[81]

43. Leaves essentially transversely inserted, and oriented (*2*:1; *3*:*2*).....44

43. Leaves clearly succubously inserted, ± obliquely oriented (*2*:3-4; *3*:4-5). 58

Leaves ± transversely inserted and oriented (couplets 44-57).

44. Leaves (at least in part) 3-4-lobed.....45

44. Leaves uniformly bilobed (exceptionally isolated leaves 3-lobed) (*2*:1; *3*:*2*-3). 50

45. Leaves (or most of them) 4-lobed; underleaves very large, usually *2*-lobed. 46

45. Leaves (or most of them) 3-lobed; underleaves small or absent.....48

46. Leaf lobes sublinear, only 3-5 cells wide at base; rhizoids scarce, only at bases of underleaves; leaf cells equally thick-walled, elongated; (capsule wall *2*-stratose).....*Lophochaete*[82]

46. Leaf lobes ovate to triangular, many cells wide at base; rhizoids frequent, scattered over postical face of stem; median leaf cells not strongly elongated; (capsule wall 4-5-stratose).....47

47. Underleaves very large, almost as long as leaves; leaves with lobes channeled, suberect or erect, pluridentate at base.....*Chandonanthus*[83]

47. Underleaves less than half the length of leaves (*3*:5); leaves with lobes not channeled, spreading, entire at base (although postical leaf base ciliate).....*Lophozia* subg. Orthocaulis[84]

48. Small underleaves present; trilobed leaves with antical lobe clearly the larger; antical end of leaf insertion oblique, running *down* the stem. .....*Lophozia* subg. Orthocaulis[85]

48. Underleaves lacking; trilobed leaves with antical lobe smaller or equal to others; antical half of leaf insertion *transverse, or running up* toward stem apex.....49

49. Stem with cortical cells narrow, linear; leaves truncate-trilobate at summit, the lobes equal, short, obtuse or subacute; leaf-insertion broadly U-shaped. .....*Saccobasis*[86]

49. Stem with cortical cells only *2*-5 × as long as wide; leaves asymmetric, obliquely trilobed at apices (when gemmae-free), with lobes sharp, the antical usually a mere tooth before the apex; dorsal end of leaf insertion transverse. .....*Tritomaria*[87]

50. Leaf lobes running out into slender cilia.....*Nowellia*

50. Leaf lobes obtuse, acute, or rounded (*3*:1-3).....51

51. Leaf lobes acute or subacute, somewhat unequal, the antical smaller (*3*:1-3); leaves somewhat, but loosely complicate (*3*:2a); leaves usually with vineous to reddish or purplish gemmae; underleaves absent (*3*:3). 52

51. Leaf lobes equal or nearly so, not complicate (*2*:1); gemmae absent or smoothly ovoid or ellipsoidal (exc. *Prionolobus*).....53

52. Plants small, 0.3-1.0 mm. wide; leaves clearly elongate, strictly transversely inserted, the antical base not decurrent (3:2-3); leaves with postical lobe clearly spreading (3:3).....*Eremonotus*[88]

52. Plants more robust: 1.0-2.5 mm. wide; leaves (in ours) little elongated, about as wide as or wider than long, the antical base more or less decurrent (3:1); postical lobe of mature leaves more or less incurved (3:1).....*Anastrophyllum*[89]

53. Leaf cells equally thick-walled, devoid of distinct trigones; oil bodies lacking, or minute and 4-several per cell; leaves usually bilobed 0.45-0.85 their length (2:1); perianth elongate, freely exserted beyond bracts....54

53. Leaf cells collenchymatous (at least in leaf middle), the trigones often bulging; oil bodies large, conspicuous, 2-3 per cell; perianth absent, or a short tube hidden between bracts; underleaves usually lacking.....56

54. Underleaves large and conspicuous, ovate-trangular, nearly as long as leaves.....*Pleuroclada*

54. Underleaves absent or very small.....55

55. Cells very small, 6-15 μ wide at base of lobes; cells with oil bodies; stem without a distinct hyalodermis.....*Cephaloziella*[90]

55. Cells larger, usually (12)15-40 μ wide at base of lobes; cells without oil bodies; stem with a hyalodermis of large, pellucid cells.....*Cephalozia*

56. Leaves closely imbricate, erect-appressed; perianth essentially lacking (5:8); usually whitish to greyish.....57

56. Leaves distant to approximate, ± spreading, often pectinately so (5:4); normally retaining a short, tubular perianth and high perigynium (1:7; 5:4).....*Marsupella*[91]

57. Large perigynium present, at an angle to axis (as in 5:7); underleaves distinct but minute, largely hidden among rhizoids; plants freely stoloniferous, closely adnate to substrate and creeping.....*Prasanthus*

57. Perigynium absent or vestigial (5:8); underleaves normally lacking; plants often without stolons, closely appressed in erect tufts.....*Gymnomitrium*[92]

Leaves lobed or dentate, succubously inserted and oriented (couplets 58-75).

58. Underleaves of sterile shoots obvious, often large (5:5); without postical stolons.....59

58. Underleaves of sterile shoots vestigial or absent (in *Cladopodiella* with small underleaves; this genus has stolons).....64

59. Rhizoids restricted to a small field at the bases of (some) underleaves; underleaves bifid, usually with 1(2) teeth on the outer margins.....*Lophocolea*

59. Rhizoids scattered over the postical face of stem (3:10).....60

60. Leaf margins variously dentate but not lobed at apex (1:8; 2:5), rarely nearly entire; antical leaf margin folded under, especially in drying.....*Plagiochila*

60. Leaf margins entire except that apex is clearly bilobed; antical leaf margin ± flat (5:5).....61

61. Underleaves ovate to ovate-lanceolate, usually entire, usually narrowly connate with base of lateral leaves (on one side); perianth and perigynium both developed (5:5).....*Harpanthus* and *Nardia p.p.*[94]

61. Underleaves bilobed or dentate, or ciliate, free from lateral leaves.....62

62. Underleaves regularly divided almost to base into *2* parallel, lanceolate segments; branches all postical; perianth absent; plant opaque, yellowish-green; (no purplish pigment; oil bodies small, 8-12 per cell). ..... *Geocalyx*

62. Underleaves various, more or less ciliate or dentate; branches all lateral; perianth distinct; not opaquely yellow-green.....63

63. Leaves much broader than long, asymmetrically bilobed for only 0.1-0.15 their length; underleaves regularly bifid, with ciliate margins, often purplish; plants with a distinct perigynium at an angle with the stem; arctic. ..... *Mesoptychia*[95]

63. Leaves usually as long or longer than broad, nearly symmetrically bilobed for 0.2-0.35 their length; underleaves irregularly divided and ciliate, never purplish; perigynium lacking.....*Lophozia* subg. Leiocolea[96]

64. Leaves (or some of them) bearing more than *2* lobes (*3*:4), or irregularly lobed, or bearing several to many teeth, but never with marginal rhizoids. 65

64. Leaves uniformly and simply bilobed (but in *Acrobolbus* the margins of the leaf, including lobes, may bear rhizoids) (1:3; *2*:4).....66

65. Leaves bearing several irregular, filiform (caducous) lobes, or spinose-dentate on margins, or bilobed and/or with accessory spinose teeth; asexual reproduction, if any, by caducous leaves or by propagula; never with true gemmae; rhizoids usually lacking on leafy shoots. ..... *Plagiochila*[97]

65. Leaves bearing *3*-4 subequal lobes (*3*:4), without accessory teeth (except for occasional cilia of postical base); asexual reproduction, if any, by true gemmae; rhizoids abundant on leafy shoots. .....*Lophozia*, subg. Barbilophozia and Orthocaulis[98]

66. Most branches, or at least the sexual branches, postical in origin; leaf cells non-collenchymatous, becoming equally thick-walled.....67

66. Branches uniformly lateral in origin (*2*:*2*-3).....69

67. Stem with a hyalodermis of large, pellucid cells; perianth trigonous, long and slender; oil bodies lacking; underleaves lacking.....*Cephalozia*

67. Stem with cortical cells opaque, small; oil bodies present; minute underleaves usually present.....68

68. Postical flagella present; leaves with rounded or obtuse lobes; perianths trigonous, elongate and slender; plants medium-sized, over 500 μ wide. ..... *Cladopodiella*

68. Postical flagella lacking; leaves with acute or subacute lobes; perianth usually bearing 4-5 plicae; plants very small 250-600 μ wide. ..... *Cephaloziella*[99]

69. Leaves, or some of them, developing marginal rhizoids; plants bluish-green, opaque; leaf cells closely and conspicuously verrucose. ..... *Acrobolbus*

69. Leaves uniformly without marginal rhizoids; leaf cells smooth or obsoletely verruculose.....70

70. Leaves oblong, distant to approximate, narrowed basally, freely caducous. .....*Plagiochila* (*tridenticulata*)[100]

70. Leaves broad at base, persistent.....71

71. Minute plants, only on palm trunks; gemmae none; perianth caducous, flaring to the wide, truncate mouth (1:3); cells minute, 15-17 μ wide at leaf middle, leptodermous and without trigones; subtropical and tropical. ..... *Chonecolea*[101]

71. Medium-sized, 500-2500 μ wide; plants never corticolous; perianths narrowed to the apex, persistent; cells larger, 20-40 μ wide at midleaf; arctic to temperate.....72

72. Leaves with postical margin sharply reflexed, the apices merely shallowly emarginate, with reddish-purple gemmae; west coast. ..... *Anastrepta*

72. Leaves with postical margin not reflexed (2:4); 0.2-0.5 bilobed, never with purple gemmae.....73

73. Underleaves normally lacking, or present merely as stalked slime papillae (2:4); plants not very fleshy; perigynium absent; leaf cells with several to numerous small oil bodies.....74

73. With small underleaves (5:5); plants fleshy, with thick, soft stems; perigynium distinct (5:5); cells with 2-3(4-5) very large, granular oil bodies; cells with large, bulging trigones; gemmae none. .....*Nardia* (*lescurii, insecta*)

74. Leaves with lobes blunt to rounded (2:2-4); gemmae absent (or rare); cells with trigones small or absent.....75

74. Leaves with lobes acute to angulate; gemmae usually abundant. .....*Lophozia* subg. Lophozia, Isopaches and Massula (*p. p.*)[102]

75. Leaves nearly flat and nearly horizontal; plants never blackish. .....*Lophozia* subg. Massula (*obtusa*)[103]

75. Leaves ± concave, often hemispherical, oblique; plants usually blackish, often appearing scorched.....*Gymnocolea*[104]

Leaves entire and unlobed (*couplets* 76-88).

76. Leaves clearly opposite, margined with thick-walled cells; rhizoids only at underleaf bases (5:6-7).....*Arnellia*

76. Leaves clearly alternate (1:10).....77

77. Postical leafless stolon present; underleaves small or minute, bearing slime papillae. (Leaves either margined with thick-walled cells, or plants developing gemmae).....*Odontoschisma*

77. Postical stolon never developed (but sometimes with stolon-like branches from leaf axils); underleaves, if present, without numerous slime papillae. 78

78. Cells of leaf middle 45-50 μ wide or more, with coarse, knot-like trigones; gemmae present at tips of unreduced leaves; underleaves obvious, lanceolate. .....*Mylia*[105]

78. Cells of leaf middle 36 μ wide or less, without or with small (never coarsely bulging) trigones; gemmae absent (in *Jungermannia* sometimes present, on margins of minute, reduced leaves).....79

79. Rhizoids restricted to small areas at the bases of the underleaves, or to conspicuous specialized cushioned areas at the bases of the underleaves; underleaves large and conspicuous, lanceolate or bifid.....80

79. Rhizoids scattered over postical side of stem; underleaves absent or formed of a few minute cilia (larger and lanceolate only in *Nardia*, which has perfectly orbicular leaves and cells with bulging trigones).....83

80. Rhizoids from the margins of large, complex, often purplish cushioned areas below the underleaves; marginal cells larger than the intramarginal, the cells with large trigones; perigynium distinct; west coast. ..... *Gyrothyra*[106]

80. Rhizoids in small tufts from the very bases of the underleaves, without purplish pigmentation; marginal cells not differentiated; all cells with vestigial or small trigones; perigynium none (1:10).....81

81. Underleaves entire; lateral leaves obdeltoid and obcuneate, nearly transverse, freely caducous; cells with obvious, often slightly bulging trigones. ..... *Anomylia*[107]

81. Underleaves bifid, often with 1-2 lateral cilia; leaves oblong to rounded-quadrate, strongly obliquely inserted, persistent; cells leptodermous or with small, inconspicuous trigones.....82

82. Perianths short, not or barely exceeding calyptra, on short, lateral shoots. .....*Chiloscyphus*

82. Perianth long, far exceeding calyptra, on long leafy shoots (1:10). ..... *Lophocolea*[108]

83. Underleaves present, small, undivided, lanceolate; with a well-developed perigynium, usually at an angle to the axis (5:5) leaves perfectly orbicular. ..... *Nardia*

83. Underleaves of sterile shoots lacking or divided into several cilia; perigynium absent (1:6), or continuous with stem.....84

84. Perianths not subtended by a perigynium, strongly laterally compressed, the mouth widely truncate (1:6); with distinct but minute underleaves, formed of 2-several short cilia tipped by slime papillae.....85

84. Perianths not laterally compressed (or subtended by a pronounced perigynium); underleaves of sterile stems lacking or reduced to an unlobed vestige. 86

85. Cells with 3-9(18) small, relatively inconspicuous, segmented oil bodies, the cells relatively pellucid; leaves often bearing minute teeth (1:6), their antical margins usually deflexed to form a convex fold (more pronounced in drying); dioecious and usually sterile..... *Plagiochila*[109]

85. Cells with 2-5 very large, finely granulose oil bodies, nearly filling cell lumen, the cells opaque; leaves entire, rarely retuse, the antical margin flat; monoecious and usually fertile.....*Pedinophyllum*[110]

86. Perianth at maturity clearly evident, not hidden between bracts, usually slightly to longly exserted (1:4); oil bodies finely granulose to almost homogeneous; female bracts not margined by slime papillae (1:4)....87

86. Perianth at maturity a short, laterally compressed ring or tube, completely hidden between the mussel-shaped, medially connivent female bracts, which form a bilabiate pseudoperianth (5:3); oil bodies coarsely and irregularly segmented; margins of female bracts bordered by slime papillae (5:2). .....*Cryptocolea*[111]

87. Bases of female bracts and perianth-mouth bearing teeth or cilia; a large, conspicuous bracteole present; rhizoids colorless, but rest of plant often dull reddish-brown, never vineous-tinged.....*Jamesoniella*

87. Perianth mouth (1:4) and female bracts entire (the perianth mouth rarely wide open and obscurely lobulate, but never ciliate); bracteole absent. 88

88. Leaves rectangular, on mature shoots ± parallel-sided; perianth terete, smooth, suddenly contracted into a small beak, situated in a shallow depression; able to produce fasciculate gemmae.....*Jungermannia*[112]

88. Leaves circular to elliptical to ovate or ovate-cordate; perianth plicate, usually contracted to the mouth (1:4), if beaked, the beak not depressed; fasciculate gemmae never produced.....*Solenostoma*[113]

Order 3. Metzgerales

I. Conspectus of the Families of Metzgeriales[114]

1. Plants clearly thallose, without leaf-like lobes or leaf-like lamellae (1:15; 6:3); rhizoids colorless to brownish; capsule 2-4-valved at maturity..... 2

2. Sex organs *dorsal* on normal unmodified thalli; pseudoperianth present, often low (1:16, f), the calyptra not thick and fleshy, delicate externally; elater bearers absent, or in a tuft from base of capsule; elaters 2-4-spiral. 3

3. Pseudoperianth flap-like (1:16, f) to short-tubular, without a fringe of scales surrounding it at base, thus single, antheridia dorsal, sunken in small cavities; capsule 4-valved, spherical or nearly so; epidermal cells of capsule with distinct nodular thickenings at the angles; distinct or vestigial elater bearers attached to base of capsule; spores delicately papillate. 4

4. Thallus margins parallel-sided, unlobed; opaque auricles absent; ventral scales represented by slime papillae on 1-celled stalks; cells with numerous small oil bodies; gemmae absent. Capsule with radial or tangential bands of inner cell layer; spores precociously germinating, 70-100 μ long at time of dehiscence of capsule; elater bearers in a distinct tuft at base of capsule; capsule spherical, without a fleshy collar at base.....Pelliaceae (*Pellia*)

4. Thallus margins coarsely scalloped, with blackish auricles near the bases of the scallops; ventral scales conspicuous, lamellate; cells without oil bodies; gemmae produced on thallus surface and/or in special flasks; capsule with inner cells delicate, without thickenings; spores 1-celled at maturity, 33-45 μ; elater bearer vestigial; capsule ovoid, with fleshy collar at base.....Blasiaceae (*Blasia*)

3. Pseudoperianth double, consisting of a high, tubular involucre, surrounded by a laciniate fringe of scales; antheridia free, dorsal, subtended on 1 side by 1 or more scales; oil bodies present, small, numerous; thalli with margins unlobed, without auricles; capsule cylindrical-subovoid, usually only 2-valved, without elater bearers; neither inner or outer cells of capsule wall with localized thickenings; spores remaining 1-celled to maturity, 25-50 μ, delicately areolate. .....Pallaviciniaceae (= Dilaenaceae) (*Pallavicinia, Moerkia*)[115]

2. Sex organs situated either on short (often vestigial) lateral branches (1:14-15), or on short, reduced, postical branches, *never simply dorsal;* pseudoperianth absent: the green calyptra fleshy, thick, clavate, hairy or tuberculate; elater bearers in a tuft from *apices* of valves; elaters 1-spiral; capsule wall 2-stratose; gemmae (6:6-7) or broodbodies (6:1-3) often present..... 5

5. Thalli lacking a sharply defined midrib, opaque, the wings pluristratose, gradually thinner laterally (6:7), not hairy at margins; cells with distinct, finely segmented oil bodies; sex organs on short lateral

branches (the gynoecial often appearing laterally sessile) (1:14-15); capsule longly ovoid; asexual reproduction by 2-celled gemmae arising *within* epidermal cells (6:6-7).
.....RICCARDIACEAE (= Aneuraceae) (*Riccardia, Trichostylium*)[116]

5. Thalli with a sharply defined costa flanked by wholly unistratose wings (6:3); margins usually with free development of 1-celled hairs (6:3); oil bodies absent, or merely represented by minute oil droplets; sex organs dorsal on very short postical branches; capsule spherical; asexual reproduction by thallose broodbodies arising from peripheral cells (6:1-3).....METZGERIACEAE (*Metzgeria*)

1. Plants essentially leafy, the leaves free (1:1), or united so that they are reduced to dorsal, transverse, leaf-like lamellae; rhizoids often purplish; cells with distinct, fine-segmented oil bodies; sex organs dorsal on thallus (1:1-2); sporophyte with capsule spherical (1:2), irregularly dehiscing into fragments at maturity; without elater bearers; elaters 2-3-spirial.
....FOSSOMBRONIACEAE (=Codoniaceae) (*Fossombronia, Petalophyllum*)

II. ARTIFICIAL KEY TO GENERA OF METZGERIALES

1. Plants obviously thallose: not bearing free lateral leaves or dorsal, leaf-like lamellae (1:15; 6:3, 7); rhizoids colorless or brownish..... 2

1. Plant leafy: the largely unistratose, delicate leaves free to axis (1:1), or connate so that they appear to be mere transverse, dorsal, leaf-like lamellae; plants rather small, 1-3.5 mm. wide..... 8

2. Thallus margins with bristle-like hairs (6:3); midrib sharply discrete, narrow, the lamina on either side uniformly unistratose; sex organs on short ventral branches; seta of 3 rings of cells, of 4, 8 and 16 cells each. ..... *Metzgeria*

2. Thallus margin naked; midrib gradually passing into the thallus wings which are not uniformly unistratose; reproductive organs dorsal on main thallus or short lateral branches (1:14-16); seta otherwise..... 3

3. Plants freely 2-3 × dichotomously or irregularly branched (6:7), the divisions narrow (usually 0.5-1.2 mm. wide); cells (or some of them) with 1-2(3-5) very large oil bodies; 2-celled endogenous gemmae (6:6-7) sometimes produced; seta of 8 outer, 4 inner cell rows (7:9).....*Riccardia*

3. Plants slightly branched the divisions largely 3.5-8 mm. wide, sometimes broader; cells with many small oil bodies, or absent; without endogenous 1-2-celled gemmae; seta of an indefinitely large number of cell rows (7:1-2). 4

4. Lateral thallus margins not scalloped; without scattered swollen blackish spots; ventral scales absent; gemmae never present; cells with many small, spherical oil bodies..... 5

4. Thallus margins scalloped or shortly lobed at the bases of the lobes with blackish swellings (auricles); with flat, ovate ventral scales; many-celled gemmae present; oil bodies lacking; midrib distinct.....*Blasia*

5. Thallus without a defined midrib, gradually thinner from median to lateral portions, yellow-green, opaque, turgid, thick and brittle; sex organs on short lateral branches.....*Trichostylium*[116]

5. Thallus with a distinct midrib, pure to deep green, the wings transparent to translucent, quite thin and herbaceous, not brittle; sex organs dorsal on the main thallus..... 6

6. Thallus with a sharp costa bearing a central strand of thick-walled small cells (visible as an opaque line by transmitted light); (antheridia dorsal, surrounded by scales; plants with an outer involucre of fimbriate scales, and eventually a long, tubular inner involucre).....*Pallavicinia*

6. Thallus with costa of ± uniform cells, not with a single conspicuous opaque strand of cells..... 7

7. Thalli ± undulate, often crispate, freely branching; antheridia dorsal on thallus, each with a toothed scale at base; archegonia surrounded by a group of fimbriate laciniae (and, with time, a tubular pseudoperianth). ..... *Moerkia*[115]

7. Thalli ± flat, sparsely branching or simple; antheridia sunken into small dorsal pits, appearing like smooth pustules on dorsal surface of thallus; archegonia surrounded by a short, single involucre or involucral flap (1: 16, f). .....*Pellia*[117]

8. Leaves free (1:1); rhizoids purplish.....*Fossombronia*

8. Leaves connate, so that only their antical margins appear free as transverse lamellae; rhizoids colorless to brownish.....*Petalophyllum*

Order 4. Sphaerocarpales

Plants essentially leafy, consisting of a delicate, rosette-like gametophyte, divided into radiating segments, each of which is divided into alternate, unistratose, subquadrate to subrotund leaf-like lobes; central, undivided section of segments not terete, not bearing a wing or wings; oil cells absent; terrestrial. ....Suborder Sphaerocarpinae. Sphaerocarpaceae (*Sphaerocarpus*)[118]

Plants consisting of a terete axis bearing two rows of small, leaf-like scales and a conspicuous, undulate dorsal wing or two wings); oil-cells scattered; aquatic or subaquatic.....Suborder Riellinae. Riellaceae (*Riella*)

Order 5. Marchantiales

I. Conspectus of Suborders and Families of Marchantiales[119]

1. Elaters absent; capsule wall delicate, without thickenings, resorbed at maturity; sporophyte without foot or seta; archegonia scattered singly on thallus or in irregular groups, immersed within the main thallus segments; vegetative thalli usually small: usually 0.5-2.5(4) mm. wide, closely furcate with divergent branches, thus forming partial or whole rosettes; (egg cell usually dividing to form quadrants). .....Ricciinae. Ricciaceae (*Riccia, Ricciocarpus, Oxymitra*)[121]

1. Elaters present (reduced in *Corsinia*); capsule wall persistent and not disintegrating at maturity; sporophyte with distinct foot and seta; archegonia united in groups that are elevated on archegoniophores (except in *Targionia* and *Corsinia*); vegetative thalli usually robust: usually 2-10 mm. wide or more, loosely or scarcely branching and thus not forming distinct rosettes. 2

2. Sporophytes occurring singly and sessile on the chief thalli, not united in archegoniophores; (thalli with air chambers in a single layer, with simple chlorophyllose filaments arising from plane floor of air chambers; pores simple. 3

3. Sporophytes at anterior edge of thallus, the delicate, smooth calyptra surrounded by a mussel-shaped involucre; elaters distinct; capsule walls with annular thickenings; thalli with pores surrounded by several

rings of differentiated cells, the epidermal cells all with strong trigones; (egg cell dividing to form a uniseriate row, of the "filament" type).....TARGIONIINAE. TARGIONIACEAE (*Targionia*)

3. Sporophytes dorsal, not surrounded by involucres, the calyptra firm, fleshy, armed with papillae or protuberances; spiral elaters absent; capsule wall without thickenings; dorsal epidermis of thallus delicate, without trigones, the pores surrounded by 1 ring of almost undifferentiated cells; (egg cell dividing to form quadrants).. .....CORSINIINAE. CORSINIACEAE (*Corsinia*)

2. Sporophytes in groups, elevated above the thallus on long or short stalks, associated in archegoniphores; elaters always distinct; calyptra delicate, not papillose. Suborder MARCHANTIINAE..... 4

4. Pores compound, both on thallus and archegoniophores, the peripheral cells in several rings, their radial walls not thickened (or in *Dumortiera* pores lacking), with a flat floor from which arise chlorophyllose filaments;[120] antheridial receptacles stalked; stalks of archegoniophores with 2-4 rhizoid furrows; spore-elater ratio more than 4:1; archegoniophores variable, but involucres each with several archegonia. .....MARCHANTIACEAE (*Marchantia, Preissia, Bucegia, Dumortiera*)

4. Pores of thallus well developed, simple, surrounded by cells oriented in a single layer; antheridial receptacles sessile (in some instances very loosely organized and the antheridia scattered on thallus surface); stalks or archegoniophores with 0, 1 or 2 rhizoid furrows; spore-elater ratio 4:1; archegoniophores with each involucre with a single archegonium (except in *Lunularia*, which is normally sterile)..... 5

5. Pores simple, stellate, the peripheral cells in 1 ring, with ± thickened radial walls; ventral scales with a single, tapering ill-defined appendage; androecia (except in *Peltolepis*) of a series of loosely organized antheridia, each antheridium with a conspicuous elevated ostiole above it; spores with coarse, contiguous papillae; capsule wall splitting irregularly, with well-defined annular bands; air chambers in several layers, the walls forming the chlorenchyma, without chlorophyllose filaments; archegoniophores conspicuously divided into (2-3)4-7 deeply bilabiate involucres, each with a single archegonium. .....CLEVEACEAE (*Athalamia* [= *Clevea*], *Sauteria, Peltolepis*)[122]

5. Pores of thallus not stellate, the radial walls not prominently thickened (except sometimes in *Plagiochasma*, which see); ventral scales normally with sharply-defined appendages, sometimes constricted basally at juncture with body of scale; androecia usually in the form of sharply-defined disks; spores usually regularly or irregularly areolate; capsule wall without annular thickenings (except in *Conocephalum*)..... 6

6. Capsule spherical, opening by a lid, the remainder of the capsule forming a persistent urn-shaped structure, lacking annular bands, shortly pedicellate and not exserted; thalli with air chambers in 2-several layers, often ± subdivided by secondary walls or cell plates, lacking free, simple, green filaments, the aerenchyma layer not with a plane floor; gemmae lacking; ventral scales with 1-3 linear to lanceolate, non-constricted appendages.....GRIMALDIACEAE (= Reboulliaceae) (*Mannia, Cryptomitrium, Plagiochasma, Reboulia, Asterella*)

6. Capsule opening by 4-8 valves, ovoid to elongate-ovoid; thallus with air chambers in a single layer, not subdivided, the chlorophyllose cells

in short, erect, simple filaments arising from the level floor of the aerenchyma; ventral scales each with a single, semicircular appendage that is constricted at base..... 7

7. Capsule short-ovoid, dividing to base into 4 regular valves, on an elongate seta (thus exserted beyond involucres); cells of wall without annular bands; archegoniophores with 4 distinct involucres, free almost to base, thus deeply 4-lobed and cruciate, archegoniophores dorsal on thallus, the stalk lacking a rhizoid furrow; gemmae present. .....LUNULARIACEAE (*Lunularia*)

7. Capsule elongate-ovoid, tearing to middle into *ca.* 8 irregular valves, shortly pedicellate; cells of wall with angular bands; archegoniophores with 6-8 closely connate involucres, scarcely lobed, conoidal, archegoniophores terminal in origin, the stalk with 1 rhizoid furrow; gemmae absent.....CONOCEPHALACEAE (*Conocephalum*)

II. ARTIFICIAL KEY TO GENERA OF MARCHANTIALES

1. Thalli small to very robust: segments (thallus branches) usually 2.5-20 mm. wide, without sharply impressed median furrows; thalli diffusely or scarcely branching, never forming compact rosettes; (usually with externally conspicuous archegonial or antheridial receptacles, the former usually, the latter sometimes elevated on stalks)..... 2

1. Thalli small or medium-sized: segments usually 0.5-4 mm. wide, the segments usually distinctly longitudinally furrowed dorsally or sharply sulcate, at least in distal portions of segments; thalli closely branched, forming usually perfect or partial rosettes; (antheridia and archegonia always sunken in the vegetative thalli, not or scarcely evident externally; ventral scales absent or simple and non-appendiculate).....17

2. Thalli with distinct air chambers and a well-developed dorsal epidermis bearing distinct pores; ventral scales well developed, usually distinctly appendiculate; thalli light to greyish-green, quite opaque; without rigid, marginal and submarginal cilia..... 3

2. Thalli without air chambers, with dorsal epidermis absent or vestigial, lacking pores; ventral scales obsolete; thalli robust (1-2 cm. wide), deep green, somewhat translucent, with rigid, cilium-like, marginal and submarginal bristles. .....*Dumortiera*

3. Pores of thallus simple, formed of a single cell layer; antheridia never united into stalked groups..... 4

3. Pores of thallus compound, formed of several superimposed tiers of cells forming a chamber, thus "barrel-shaped"; antheridia united into groups elevated on a distinct stalk.....15

4. Air chambers in a single layer, the chlorenchyma formed by simple filaments arising from a flat floor..... 5

4. Air chambers in several layers, ± irregular, the chlorenchyma formed by the walls of the chambers, and/or supplementary walls or cell plates, the boundary between chlorenchyma and ventral tissue not forming a plane floor, but irregular and gradually transitional..... 8

5. Plants very large, 8-20 mm. wide × 3-20 cm. long; ventral scales colorless or violet, each with a single short, obtuse to rounded, reniform broad appendage that is strongly constricted at base; (archegoniophores stalked; gemmae present or absent)..... 6

5. Plants small: 3-5 mm. wide × 1-4 cm. long; ventral scales each with a ± tapering or a uniseriate appendage, not basally constricted; (archegonia single, and sessile on thallus; gemmae absent)..... 7

6. Without gemmae; thalli very robust and leathery, the dorsal surface coarsely hexagonally areolate, dull; plants strongly fragrant. ..... *Conocephalum*

6. Gemmae in crescentic receptacles; thalli not leathery, the dorsal surface nearly smooth, slightly shiny; plants almost odorless..... *Lunularia*

7. Ventral scales small, with minute appendages, colorless and obscure; pores of thallus surrounded by a single ring of undifferentiated cells; epidermal cells thin-walled, without trigones..... *Corsinia*

7. Ventral scales large, blackish-purple, with distinct, tapering appendages; pores surrounded by 2-3 circles of differentiated cells; epidermal cells with strong trigones. ..... *Targionia*

8. Female receptacles (archegoniophores) ***dorsal*** on thallus, their stalks without a rhizoid furrow; pores surrounded by 1, rarely 2 rings of differentiated cells whose radial walls are usually thickened (pores thus ± stellate). 9

8. Female receptacles arising from an apical notch of thallus segments or branches, their stalks with 1-2 rhizoid furrows; pores various..... 10

9. Ventral scales (and thallus tissue) with scattered oil cells; cells of dorsal epidermis usually with large to bulging trigones; capsule wall without annular bands. ..... *Plagiochasma*

9. Ventral scales and thallus tissues without oil cells; dorsal epidermis delicate, without trigones; capsule wall with annular thickenings. ..... *Athalamia* (*Clevea*)[122]

10. Pores surrounded by a single ring of differentiated cells, strongly stellate-thickened along radial walls; capsule wall with annular thickenings; archegonial receptacles very deeply 2-5(6-7)-lobed, when mature often cruciate. 11

10. Pores surrounded by 2-several rings of cells whose radial walls are not conspicuously thickened; capsule wall without annular thickenings; receptacles not or shallowly lobed, never cruciate..... 12

11. Thallus and ventral scales without oil cells; female receptacle with stalk bearing 2 rhizoid furrows; thalli firm, ± purplish tinged on margins. ..... *Peltolepis*[123]

11. Oil cells present; receptacles with stalk bearing 1 rhizoid furrow; thalli spongy, light green, with colorless ventral scales (even in sun). ..... *Sauteria*[124]

12. Pores (when mature) surrounded by 4-5 concentric rings of cells, each usually formed of 8 cells; receptacles weakly convex, usually divided into 4-7 nearly horizontal, discrete lobes (each ending in a bilabiate involucre); paroecious; without pseudoperianth..... *Reboulia*

12. Pores surrounded by 2-3(4) concentric rings of cells, each formed of (4)5-7(rarely 8) cells; receptacles varying from very shallowly lobed to subentire. 13

13. Pseudoperianth absent (but receptacles often with scales at apex of stalk that may be confused with them)..... 14

13. Pseudoperianth present, in the form of a sheath around each sporophyte that divides into lanceolate, conspicuous segments; receptacles hemispheri-

cally convex to conoidal, their margins not elaborated as a thin wing. ..... *Asterella*

14. Receptacles strongly convex, their margins not elaborated as a spreading, horizontal wing, shallowly lobed (each lobe with a sporophyte); dioecious or autoecious.....*Mannia* (= *Grimaldia*)[125]

14. Receptacles disk-like, the centre convex but the thin horizontal margins elaborated as an unlobed wing extending over and far beyond the sporangia; paroecious. .....*Cryptomitrium*[126]

15. Ventral scales deep purplish, in two rows; gemmae absent; female receptacles shallowly 4-5-lobed on the margins, or hardly so; ventral scales without oil cells (or at most with 1-2).....16

15. Ventral scales colorless or pinkish, in 4-6 rows; gemmae in distinct, cup-like receptacles; female receptacles very deeply divided into 5-9 lobes or segments; ventral scales with oil cells. (Air chambers with photosynthetic filaments in one layer).....*Marchantia*

16. Thalli with air chambers in a single shallow layer, with free chlorophyllose filaments arising from floor; thalli in cross-section weakly costate. .....*Preissia*

16. Thalli with air chambers in 1-2 layers, empty, without chlorophyllose filaments; thalli strongly and sharply costate.....*Bucegia*

17. Dorsal epidermis of thallus persistent, with distinct stellate pores; ventral scales conspicuous, numerous, projecting far beyond thallus margins; sporophytes with a distinct, conically expanded involucre.....*Oxymitra*

17. Dorsal epidermis persistent or not; pores absent or simple, without differentiated cells; ventral scales usually minute and inconspicuous (except for aquatic forms of *Ricciocarpus*); sporophytes wholly hidden within the thallus, which is not expanded to form an involucre over them.....18

18. Thalli usually terrestrial (if aquatic, floating *beneath* surface); pores vestigial or absent; dorsal thallus surface and ventral scales without oil cells; ventral scales usually minute, never dentate, never sword-shaped. .....*Riccia*[127]

18. Thalli aquatic and floating on surface (rarely stranded or terrestrial); persistent epidermis with distinct pores and oil cells; ventral scales long, conspicuous, sword-shaped, dentate and with oil cells (except in terrestrial forms). ..... *Ricciocarpus*[128]

Class Anthocerotae

Order 1. Anthocerotales

We have only one famly, the Anthocerotaceae

1. Sporophytes erect, usually 10-100 mm. high, slenderly cylindrical, longly exserted beyond the tubular perichaetia lying at their bases; sporophytes freely dividing, 2-valved (but the valves often coherent at the tip), with a central, filiform columella; sporophytes with stomata; pseudoelaters not similar in shape and size to spores..... 2

2. Spores yellowish, finely papillate; thalli deep green, relatively firm and smooth, *without* distinct lacunae within, divided into rather broad segments. .....*Phaeoceros*[129]

2. Spores black or fuscous, asperulate to spinose-areolate; thalli relatively light-green, *with* large lacunae within, the chief segments divided into small marginal segments, lobes or teeth.....*Anthoceros*[130]

1. Sporophytes horizontal to obliquely arching,1-several mm. long, fusiform to cylindrical-fusiform, at maturity only slightly emergent beyond apices of the sheathing, cylindrical perichaetia; sporophytes not or slightly and tardily dehiscent, with columella absent (in our species) or vestigial; sporophytes without stomata; pseudoelaters spherical, similar in size and shape to spores.....*Notothylas*[131]

Appendix I. An Outline of the Classification Adopted[132]

Class Hepaticae.

Subclass Jungermanniae.

Order 1. Calobryales. Family Haplomitriaceae (*Haplomitrium*).

Order 2. Jungermanniales.

Suborder Jungermanninae.[133]

Series a. Families Lophoziaceae (*Chandonanthus* [= *Temnoma sensu* Howe], *Lophozia* [Orthocaulis, Barbilophozia, Leiocolea, Lophozia, Isopaches, Massula as subg.], *Gymnocolea, Anastrepta, Acrobolbus, Saccobasis, Eremonotus* [Crossocalyx, Sphenolobus as subg.], *Anastrophyllum* [Anastrophyllum, Eurylobus as subg.] *Tritomaria, Mesoptychia*). Jungermanniaceae (*Jungermannia, Solenostoma* [Solenostoma, Plectocolea as subg.], *Nardia, Jamesoniella, Cryptocolea* and ? *Prasanthus*). Gyrothyraceae (*Gyrothyra*). Marsupellaceae (*Gymnomitrium, Marsupella* and ? *Prasanthus*). Scapaniaceae (*Scapania* [Scapaniella as subg.], *Diplophyllum, Macrodiplophyllum, Douinia*).

Series b. Families Plagiochilaceae (*Plagiochila, Mylia, Anomylia, Pedinophyllum*). Chonecoleaceae (*Chonecolea*). Lophocoleacaea (*Lophocolea, Chiloscyphus*). Harpanthaceae (*Harpanthus, Geocalyx*). Southbyaceae (*Arnellia*).

Series c. Families Hygrobiellaceae (*Anthelia, Pleuroclada, Hygrobiella*). Cephaloziellaceae (*Cephaloziella*). Cephaloziaceae (*Cephalozia, Cladopodiella, Nowellia*). Odontoschismaceae (*Odontoschisma*).

Suborder Ptilidiinae. Families Herbertaceae (*Herberta*). Ptilidiaceae (*Ptilidium*). Trichocoleaceae (*Trichocolea*). Blepharostomaceae (*Blepharostoma, Lophochaete*). Lepidoziaceae (*Lepidozia, Microlepidozia, Telaranea, Bazzania*). Calypogeiaceae (*Calypogeia*).

Suborder Radulinae. Family Radulaceae (*Radula*).

Suborder Porellinae. Families Porellaceae (*Porella, Ascidiota*). Frullaniaceae (*Frullania, Jubula*). Lejeuneaceae (*Ptychocoleus, Brachiolejeunea, Neurolejeunea, Caudalejeunea, Lopholejeunea, Mastigolejeunea, Leucolejeunea* [= Holostipae]; *Cheilolejeunea* [including Euosmolejeunea as subg.], *Ceratolejeunea, Rectolejeunea, Lejeunea* [including Microlejeunea, Chaetolejeunea as subg.], *Hygrolejeunea* [? only subg. of *Lejeunea*], *Crossotolejeunea, Taxilejeunea, Leptolejeunea, Drepanolejeunea, Harpalejeunea* [= Schizostipae]; *Diplasiolejeunea, Leptocolea, Aphanolejeuna, Cololejeunea* [= Paradoxae]).

Suborder Pleuroziinae. Family Pleuroziaceae (*Pleurozia*).

Order 3. Metzgeriales. Families Fossombroniaceae (*Petalophyllum*,

Fossombronia). PELLIACEAE (*Pellia*). BLASIACEAE (*Blasia*). PALLAVICINIACEAE (= Dilaenaceae) (*Pallavicinia, Moerkia*). RICCARDIACEAE (*Riccardia*). METZGERIACEAE (*Metzgeria*).

Subclass Marchantiae.

Order 4. Sphaerocarpales.

Suborder Sphaerocarpinae. Family SPHAEROCARPACEAE (*Sphaerocarpus* [including *Geothallus*]).

Suborder Riellinae. Family RIELLACEAE (*Riella*).

Order 5. Marchantiales.

Suborder Corsiniinae. Family CORSINIACEAE (*Corsinia*).

Suborder Targioniinae. Family TARGIONIACEAE (*Targionia*).

Suborder Marchantiinae. Families GRIMALDIACEAE (*Mannia, Cryptomitrium, Plagiochasma, Reboulia, Asterella*). LUNULARIACEAE (*Lunularia*). CONOCEPHALACEAE (*Conocephalum*). CLEVEACEAE (*Athalamia* [including *Clevea*], *Sauteria, Peltolepis*). MARCHANTIACEAE (*Marchantia, Preissia, Bucegia, Dumortiera*).

Suborder Ricciinae. Family RICCIACEAE (*Riccia, Ricciocarpus, Oxymitra*).

Class Anthocerotae.

Order Anthocerotales. Family ANTHOCEROTACEAE (*Anthoceros, Phaeoceros, Notothylas*).

In the above, the division of Jungermanniales into suborders is new. The concepts underlying this classification will be discussed at length in a future contribution, but the following seem pertinent at this point: (1) The Ptilidiinae are the most primitive of extant Jungermanniales, as is obvious from the wide variability in leaf insertion (suggesting lack of genetic rigidity). The succubous leaf type (typical of the Jungermanniae) is developed in some Blepharostomaceae such as *Temnoma* and some Ptilidiaceae such as *Herzogianthus* (see Schuster, 1957c), as well as the incubous type. (2) It is postulated that the Jungermanninae evolved from succubous-leaved Ptilidiinae, probably from genera bearing at least superficial similarities to *Temnoma* in the Blepharostomaceae and *Herberta* in the Herbertaceae. (3) Both Ptilidiinae and Jungermanninae remain "primitive" in that they have not "experimented with" development of lobuli or water sacs, with a few notable exceptions (*Lepidolaena, Trichocoleopsis* in Ptilidiinae; *Nowellia* in Jungermanninae). These two suborders also remain primitive in retaining a large number of archegonia per gynoecium. Inversely, they both have shown repeated "tendencies" to evolve a variety of specializations associated with the gynoecium (such as stem perigynia, calyptral perigynia); correlated with elaboration of the axial tissue to protect the fertilized archegonium and developing sporophyte there is often reduction (5:3-5, 7) or loss (5:8) of the perianth. (4) The prevalent restriction of the rhizoids to the underleaf bases (and/or leaf bases) in various primitive groups (Herbertaceae, Blepharostomaceae, indeed virtually throughout the Ptilidiinae; *Anthelia* (2:1) Lophocoleaceae and many Plagiochilaceae, some Southbyaceae (5:6) in Jungermanninae) suggests such restriction is primitive. Study of the ontogeny of the sporeling in such genera with "scattered" rhizoids as *Mylia* also shows that during the early development the rhizoids are restricted to the underleaf bases. Similarly, in the derivative Radulinae and Porellinae the rhizoids are always restricted, in the former to the leaf bases or keeler

region of the leaf (2:6), in the latter to the underleaf bases (4:12). The common denominator for the various modes of rhizoid distribution is a restricted rhizoid initial field found at or near the bases of all three rows of phyllidia of an essentially isophyllous shoot. This condition has been described by Schuster (1957c) for the very primitive genus *Herberta*. (5) The Radulinae and Porellinae, which are related only remotely, show fundamentally different evolutionary tendencies from those outlined above (under 3) for the Ptilidiinae and Jungermanninae. At a very early date they evolved a specialized leaf type involving a water sac or lobulus (2:6, 9; 4:4-5, 13-14); its absence in members of these groups is unquestionably a secondary feature. These two groups have also become specialized in the progressive reduction of the number of archegonia laid down in each gynoecium, although primitively there may be a higher number of archegonia. In *Radula* there are usually 5-7, rarely to 16 archegonia; in *Porella* there may be 8-10, occasionally many archegonia. There is also an almost universal tendency for the spores to germinate precociously, becoming several-celled before dehiscence of the capsule. Associated with these three very specialized features we find, contrastingly, that these groups have remained unspecialized in several other respects. The rhizoids remain "restricted," not becoming scattered over the ventral merophytes; the shoot tip, peripheral to perianth or archegonia, is never elaborated to form a stem-derived protective tissue around either sporophyte or calyptra; the perianth is never reduced or lost (1:8, 12). (6) In the Ptilidiinae, as in most very primitive groups, asexual reproduction is very rare, confined almost entirely to *Blepharostoma s. str.* (6:4, 5) and to the relatively specialized Calypogeiaceae and Lepidoziaceae. In the more derivative Jungermanninae it is common, but most frequently by means of 1-2-celled conidia-like bodies (gemmae) that are often produced in masses or fascicles (6:12); single discoid broodbodies are never developed. In the derivative Radulinae and Porellinae few-celled asexual bodies are never developed, but discoid broodbodies ("multicellular gemmae") are of widespread occurrence (6:14). (7) Branching patterns are most diverse in the more primitive groups. In the Ptilidiinae we find terminal branching of the *Frullania-*, *Acromastigum-* and *Microlepidozia*-types, as well as intercalary branches. The last may, primitively, be produced haphazardly in the axils of leaves or underleaves, as *e.g.*, in the Herbertaceae, but in the more derivative Ptilidiinae are confined either to the lateral leaves (rarely!) or more often to the underleaf axils. In the Jungermanninae the branching-modes become somewhat more restricted, to terminal branches of the *Frullania-type* (2:1, 3), or to intercalary branches from leaf and/or underleaf axils (2:1, 4). It deserves emphasis that in neither of these two groups do terminal, *Radula-* (2:6) or *Pleurozia*-type of branches ever occur. The absence of branches of this type in all extant Ptilidiinae is suggestive, since this group is so very polymorphic with respect to branching patterns (all known types of branching, except the *Radula-* and *Pleurozia*-types being found in the Lepidoziaceae!). It should be noted that in both the Ptilidiinae and the Jungermanninae, associated with less profound anisophylly and in general less perfectly procumbent growth, branches are rarely exclusively lateral in origin. Even in various Lophoziaceae, *e.g.*, *Gymnocolea* (2:2-3), where branching is almost exclusively lateral, occasionally postical intercalary branches are produced (2:4). By contrast, in the last three suborders (Radulinae, Porellinae, Pleuroziinae) postical branching is unknown, branching having become restricted to the lateral merophytes (2:6; 4:14).

The linear arrangement of these five suborders is artificial no matter what sequence is adopted. I have placed the Ptilidiinae first since they show many archaic features (limited or no anisophylly, occasional retention of antheridia in perigonal bracteoles; lack of specialized (*e.g., Radula*- and *Pleurozia*-type) branches, together with notable lack of rigidity in branching patterns; almost universal reliance on sporophytic reproduction for propagation, with gametophytic reproduction absent except in a very few specialized genera, *e.g., Blepharostoma, Bazzania, Calypogeia;* almost universal restriction of rhizoids to underleaf and/or leaf bases; gynoecia and androecia typically remaining terminal, or in the case of androecia becoming intercalary, on leading shoots, with exceptions in only the Lepidozioid-Calypogeioid derivatve sequence; variability in leaf insertion and orientation, often even within one family, *e.g.,* within the Trichocoleaceae and Ptilidiaceae. There is no need at this point to embark on an exposition of the concept that polymorphism, as in branching patterns or in leaf orientation, may be a primitive, rather than derivative feature; here I am convinced this is the case.

The suborder Jungermanninae is placed directly after the Ptilidiinae for several reasons, among them: the retention in several primitive groups such as some Lophoziaceae (*Lophozia* subg. Orthocaulis and Chandonanthus), *Anthelia,* Lophocoleaceae of very broad ventral merophytes (3:5-6; 2:7) and large underleaves (2:7); the very great similarity in branching patterns, although almost each individual group of Jungermanninae shows a tendency to develop restriction to one or two modes of branching; the retention of gynoecia with numerous archegonia (5:2, 6); a similar "ability," expressed in a wide diversity of individual groups, to elaborate the stem apex adjoining the perianth or calyptra of the fertilized archegonium (or both) into fleshy protective tissues, or perigynia (5:3-5, 8), associated with a widespread tendency for the sporophyte foot to "bore" into the tip of the axis (5:1, 5,7). It is possible that the Jungermanninae were derived from succubous-leaved Ptilidiinae, similar to such genera as *Temnoma* and *Lophochaete.* It is not impossible that the suborder originated two or more times from the Ptilidiinae. However, it is at present impossible to split the Jungermanninae into two or more sharply defined elements that have had an indubitably separate origin from discrete types in the Ptilidinnae.

A logical arrangement of the last three suborders in a linear sequence is impossible. Although the Porellinae and Radulinae are similar in their branching patterns, as well as in their fundamental leaf form and insertion, they are so different in all other respects that their inclusion in a single suborder (as in Schuster, 1953) no longer appears warranted. I have already commented (*l.c.*) on the quite unnatural and indefensible practice of placing two of the four families of Porellinae (Frullaniaceae, Lejeuneaceae) in a separate suborder, the Jubulinae. The specialized attachement of the elaters is almost the only feature that sets off this group. The non-articulate, pluriseriate seta (7:3) of the Frullaniaceae is more suggestive of the Porellaceae than it is of the Lejeuneaceae (7:7). Inversely, the spherical capsule of the Porellaceae, valvate only part way to the base, is suggestive of the fleshy and indehiscent capsule base of the "Jubulae." The precociously germinating spores of the entire suborder Porellinae are noteworthy. It has been suggested that the peculiar markings of the spore exine of the Jubulae, with the unique radial groups of papillae or verrucae, are phylogenetically important; however, the genus *Jubula* of the Frullaniaceae agrees with the Porellaceae in having uniformly granulose or papillose spores. The Goebeliellaceae, with their *Frullania*-like vegetative organization but erostrate,

wide-mouthed perianth, also serve to destroy much of the significance of a distinction between "Jubulae" and other allied families.

It is clear that the Porellinae are a natural unit, quite distinct from the Radulinae. Although the branching modes suggest a common origin, as does perhaps the tendency to possess precociously germinating spores and discoid "gemmae," the two groups do not stand in a linear relationship to each other. The total suppression of underleaves in the Radulinae (2:6; 4:4, 8) is derivative. In other respects the group is more primitive, although the absence of *Frullania*-type branches can be interpreted as derivative. Suggestive is the normal development of *Radula*-type branches (2:6) that lack a "collar" or basal ring of cells derived from the parent axis; in the Porellinae, *Radula*-type branches are absent, or else are always provided with a basal collar (6:13), with the sole exception of the inflorescence branches or innovations (2:9). However, some tropical species of *Radula* possess branches both with and without the "collar." Hence any attempt to draw a hard and fast distinction here is impossible. All in all, therefore, we must admit that these two suborders are more closely allied to each other than to any other group. And, in spite of certain specialized features of the Radulinae, this suborder is somewhat less derivative in most respects than the Porellinae. As a consequence, if an attempt is made at a linear arrangement, it seems judicious to place the Porellinae after the Radulinae.

As an "Anhang" to the preceding four suborders, I would place the unigeneric suborder Pleuroziinae. This group has no other relatives among extant groups of Hepaticae. The group is unique among leafy Hepaticae in the possession, by the mature gametophyte, of an apical cell with only two cutting faces, with the consequence that no ventral merophytes exist. Equally unique is the form of the incubous-complicate leaves. Although it might be postulated that there exists a certain superficial similarity to the leaves of the Porellinae, the incubous-complicate form has surely been derived quite independently. The reduction of the archegonia to 1-2 per gynoecium is also independently derived. It should be pointed out that in the Porellinae the leaf is usually incubously-bilobed but appears to be primitively derived from an incubously-trifid leaf. The derivation here would be from a *Mastigophora*-like or *Ptilidium*-like (4:1, 3) leaf, in which the dorsal lobe is largest, the ventral lobes progressively smaller. In many instances the ventralmost of the three lobes is not at all developed, or else is in the form of a mere slime papilla that may be terminal on a uniseriate row of cells (as in many species of *Cololejeunea*); in a few cases it is developed as a large stylus, elaborated to the fullest extent in such species as *Frullania gibbosa*. The implication is clear that *the lobule is derived from the middle lobe of a trifid leaf*. In the less specialized Pleuroziinae, such as *Pleurozia purpurea*, the leaf is also incubous-trifid, but the large dorsal "half" of the leaf is again bilobed, hence *the lobule is derived from the ventralmost lobe of a trifid leaf*. If such an interpretation is correct, the relationships between the Pleuroziinae and the Porellinae must be regarded as largely superficial and homoplastic. The unique mode of branching in the Pleuroziinae, with the branch originating near the antical base of the leaf, also bespeaks a strong and extended phylogenetic isolation of this group. In spite of the specialized leaf type, the loss of the ventral merophytes, the very specialized and unique mode of branching, other features suggest the Pleuroziinae are relatively primitive. For example, the capsule wall retains the archaic, pluristratose condition; asexual reproduction is absent; the perianth lacks the derivative features found in the Porellinae. The reduction of the arche-

gonia to 1-2 per gynoecium must be regarded as an analogous reduction, not suggestive of a closer phylogenetic relationship. An evaluation of these features suggests that the Pleuroziinae have been derived independently of the other incubously complicate-leaved groups. Since the loss of the ventral merophytes is such unparalleled feature in the Jungermanniales, I have placed the group last in the suggested linear sequence. It must be noted that growth by means of a 2-sided apical cell also appears to have been achieved in the most derivative genus of Lejeuneaceae, the thallose and unique genus *Metzgeriopsis*. The vegetative shoots here evidently grow through the agency of an apical cell with two cutting faces. It has not yet been established whether the leafy sexual branches "revert" to the ancestral growth pattern by means of apical cells with three cutting faces.

Appendix II. Annotations

1. Including all of the orders of living Hepaticae accepted in Schuster (1953) except the unigeneric, tropical Monocleales.

2. A small number of genera in the Jungermanninae have rhizoids restricted to the underleaf bases, among them: *Lophocolea, Chiloscyphus, Arnellia, Anomylia*. The first three of these have obviously succubous leaves.

3. In several genera with rhizoids very rare or virtually absent; in *Herberta* with the rhizoids from the leaves and underleaves, at least in part.

4. In a number of genera with development of lobules, but in these the lobules are wholly different in ontogeny; they are formed either from the lowermost lobe of a bilobed leaf, or from the middle lobe of a trifid leaf (the lowermost lobe then being represented by the stylus).

5. It should be pointed out here that this key is devised specifically for use with North American genera. Although the key will "work," in general, for exotic genera, there are notable cases where genera will fail to key out. A single example: The Southbyaceae are locally represented by the sole genus *Arnellia;* this has restricted rhizoids, and the Southbyaceae are keyed out (in part) on the basis of localized rhizoids. Such a restriction of rhizoids does not occur in the exotic *Southbya* or *Gongylanthus* of the same family.

6. *Lophochaete* Schuster (type: *Lepicolea fryei*) is dealt with in Schuster (1957c, 1958c).

7. For *Telaranca* and its separation from *Microlepidozia* see Schuster & Blomquist (1955). Mrs. E. Amy Hodgson (1956) in a review of New Zealand species of *Lepidozia* still treats these taxa as subgenera. Müller (1954) considers *Microlepidozia* a synonym of *Telaranca*. The basis for retaining all three genera is outlined in Schuster & Blomquist (1955).

8. In a very few genera (*Cololejeunea, Aphanolejeunea, Leptocolea*) the underleaves are lacking, but the rhizoids occur at the points where the underleaves would normally arise. In *Radula* the underleaves are also absent; in this genus the rhizoids are unique in being restricted to the lobules (ventral lobes) of the leaves. In *Pleurozia* rhizoids are absent on leafy stems, and underleaves are lacking.

9. For modern treatments of the controversial species of *Calypogeia* see Buch (1936, 1942, 1948), Müller (1947), Schuster (1949, 1953) and Buchloh (1952).

10. Underleaves absent in three genera of Lejeuneaceae (*Cololejeunea, Aphanolejeunea, Leptocolea*); these are small to minute, delicate, pale to yellow-green plants which bear rhizoids individually or in small clumps, along the stem at the points where the underleaves would normally be ex-

pected, *i.e.*, at which they have been suppressed (Schuster 1955a, 1955b, 1956). These plants differ from the Radulinae and Pleuroziinae in their remote to contiguous leaves, translucent appearance, delicacy (less than 1 mm. wide) and generally pointed leaf lobes.

11. *Ascidiota blepharophylla* occurs in Alaska; the plant has ciliate leaf margins like *P. veronicosa* ssp. *faurieri* (Steph.) Hara, erroneously referred to *Porella laevigata killarniensis* in Frye & Clark (1947, in 1937-47); for its separation from *Porella* see the key to genera; for the Alaskan *Porella vernicosa faurieri* see Ando (1955) and Hara (1956); see also annotation 67.

12. Detailed keys to the genera and a discussion of the morphology of the family are given in Schuster (1955).

13. *Arnellia, Lophocolea, Chiloscyphus* and *Anomylia* with rhizoids restricted to underleaf bases; all but *Anomylia* have strongly succubous leaves; all have distinct underleaves. *Gyrothyra* has rhizoids in a specialized cushioned area lying below the underleaves (Schuster, 1955c); in *Herberta* the few rhizoids may arise from the leaves and underleaves (Schuster, 1957c). In some cases rhizoids are rare and sporadic in development.

14. See Schuster (1955c).

15. See Schuster (1958b); *Anomylia* Schuster for *"Mylia" cuneifolia* (Hook.) Spruce. *Anomylia cuneifolia* is reported for Virginia by Schuster & Patterson (1957).

16. The rhizoids may be sparingly developed and only local; in *Herberta* rhizoids are rare and may develop from the surfaces of both leaves and underleaves (Schuster, 1957c). In a few cases, in other genera, *e.g., Geocalyx*, most of the rhizoids are near the underleaf bases, but some are always scattered over the remainder of the postical stem faces.

17. See Schuster (1949a) for a key to the genera. Note, however, that *Dianthelia* has proved to be congeneric with *Gymnomitrium*. Recent researches (unpublished) suggest that *Hygrobiella* may better be referred to the Cephaloziaceae, in which case the group will have to be known as the Antheliaceae, a name previously used by Schuster (1949a). The family Hygrobiellaceae, like the other families proposed by Müller (1939-40; 1951-56) is a *nomen nudum*.

18. I regard *Prionolobus*, given as a genus in Frye & Clark (1937-47) as a subgenus of *Cephaloziella*, following Müller (1947); see also annotation 99. The genus (or subgenus) *Dichiton*, whose type species *D. calyculatum* is reported for North America in Frye & Clark, does not occur in North America, unless *Cephaloziella rhizantha* of the southeast is ascribable to it; see Schuster (1950b). The Cephaloziellaceae are a "weak" family, perhaps better regarded as a subfamily of the Cephaloziaceae (as in Schuster, 1949a).

19. For a monograph of the North American species see Schuster (1958b).

20. For a detailed, illustrated conspectus of genera and subgenera see Schuster (1951); most of our species are also dealt with in Schuster (1952, 1953, 1953a, 1958e). Both Schuster (1951, 1953) and Müller (1939, 1942) criticize some features of the generic classification in Buch (1933) which is adopted by Evans (1935) and Frye & Clark (1946, in 1937-47).

The genus *Acrobolbus*, rather questionably assignable to the Lophoziaceae (Schuster, 1951a), is exceptional in the Lophoziaceae by its lack of a perianth. The single regional species *A. ciliatus* (*A. rhizophyllus*), is easily

identified by its proclivity to develop numerous rhizoids from the margins of the leaves.

Scapania subg. Jensenia (see Arnell, 1956) is transitional from Lophoziaceae to Scapaniaceae; see annotation *26*.

21. Choneeolea may be exceedingly difficult to tell, on a gametophytic basis, from *Cephaloziella rhizantha* (see Schuster, 1956b); *Choneeolea* is revised, for North America, in Schuster (1958a). It differs from oblique-leaved species of *Cephaloziella* in the areolate spores, wholly lateral intercalary branches, obsoletely spiral elaters, minute oil bodies numerous per cell and 8 rows of peripheral seta cells. *Choneeolea* was segregated by Grolle (1956) from *Clasmatocolea*, under which our single species, *C. doellingeri* was placed.

22. Nardia lescurii and *N. insecta* have uniformly bilobed leaves unlike the other species of the genus. These are more or less prostrate, soft, fleshy plants with nearly flat leaves.

23. Including *Dianthelia* (Schuster, 1949a), under *Gymnomitrium*; Müller (1942, 1951-56, pp. 757-804) gives a much more modern and thorough review of the species than Frye & Clark (1943, in 1937-47). See Schuster (1957b) for the recently described *Marsupella paroica*.

The genus *Prasanthus* has recently been transferred to the Jungermanniaceae by Müller (1951-56) and Arnell (1956). It agrees with *Gymnomitrium* in the densely imbricate leaves, the shoots being compact, worm-like and julaceous. This transfer to the Jungermanniaceae is perhaps based on the presence of small underleaves, which are supposedly absent in Marsupellaceae. However, distinct, if vestigial, underleaves are occasionally discernible in *Gymnomitrium steerei* (Schuster, 1949a). *Prasanthus* has an oval capsule; in the Marsupellaceae it is generally spherical; in the Jungermanniaceae it is oval. On this last basis the genus perhaps belongs in the Jungermanniaceae. However, *Prasanthus* has virtually transversely inserted and oriented leaves, as in the Marsupellaceae. The position of this genus remains doubtful.

The African *Gymnomitrium elgonense* Arnell (Arnell, 1956a) appears to be identical with *G. steerei* of the Southern Appalachians.

24. For revision of the family in North America see Schuster (1958b). *Plagiochila* differs from the Jungermanniaceae in the often minute but distinct, more or less ciliate to laciniate underleaves; *Mylia* differs in the very large leaf cells (45 μ wide or more in leaf middle), in the very dense rhizoids, and in the ability to form gemmae in fascicles from the upper leaves.

25. Plectocolea is considered here a subgenus of *Solenostoma*, with *Jungermannia* a monotypic genus, based on *J. lanceolata* (see Schuster, 1953); for *Cryptocolea*, see Schuster (1953), who states it is intermediate in some features between Plagiochilaceae and Jungermanniaceae. Müller (1939-40) uses the invalid family name Nardiaceae.

26. Most of our species of *Scapania* are treated in detail in Schuster (1951, 1951b, 1953); *Macrodiplophyllum* (Buch) Persson was established for *Diplophyllum* subg. Macrodiplophyllum by Persson (1949); see also Müller (1944) for valuable notes on a variety of species.

Scapania subg. Jensenia (see Arnell, 1956, p. 173) is transitional to the Lophoziaceae in form, since it lacks all trace of a true "keel." The leaves are hemispherically concave to loosely complicate-bilobed. A species of this subgenus has also been described under the genus *Marsupella*. Jensenia differs from the Lophoziaceae, and agrees with the Scapaniaceae, in the constantly intercalary branching. Almost all Lophoziaceae produce at least

occasional terminal branches, although these are very rare in some genera (*Tritomaria, Anastrophyllum*). The oval, non-angulate gemmae of Jensenia also are suggestive of the majority of Scapaniaceae; such gemmae very rarely occur in Lophoziaceae. A species of this subgenus was collected by the author in northern Ellesmere Island; it is possibly identical with *Scapania* (J.) *lapponica* (Arn. & Jens.) Steph. No other occurrences of the subgenus for the Western Hemisphere are known.

Various other *Scapaniae* often have weakly keeled leaves, and may, because of this, be "keyed" to the Lophoziaceae, from which family they are presumably derived. The unequally complicate-bilobed leaves, the usual development of at least traces of marginal teeth of the leaves, the total lack of underleaves, the universal development of gemmae (usually non-angulate in form) and the lateral, axillary branching serve to place these species in the Scapaniaceae.

I have reduced the genus *Scapaniella* of Buch (1928) to a subgenus of *Scapania* (Schuster, 1949, 1953). Müller (1951-56) goes even further and reduces it to a mere section of the genus. It is maintained in Frye & Clark.

27. For example, it is almost impossible to separate the dead gametophytes of *Chonecolea* = "*Clasmatocolea*" from those of some species of *Cephaloziella;* see, for a separation, Schuster (1956a), and the detailed study of *Chonecolea* in Schuster (1958a).

28. Although the most common and obvious mode of asexual reproduction is by means of conspicuous, often differentially pigmented gemmae, many other modes occur that are more difficult to ascertain. The Plagiochilaceae often produce propagula from the leaf cells (usually only from the lower surfaces); Lejeuneaceae often produce discoid "gemmae" from the lower, rarely also upper leaf surfaces. Many genera drop their leaves, etc.

29. Gemmae have been reported in our species of *Ptilidium, Lepidozia* and *Microlepidozia.* These reports are all very old and wholly untrustworthy, although, in part, repeated in Frye & Clark (1937-47). Although Mrs. Hodgson (1956) reports gemmae in a New Zealand species of *Lepidozia,* I am of the opinion that the occurrence of gemmae in true members of these genera is as yet to be effectively demonstrated.

30. For detailed accounts of asexual reproduction in these species see Schuster (1957a, 1958b).

31. *Anomylia* Schuster = *Mylia* auct., *p.p.* (*"Mylia cuneifolia"*); for an account of this species and its asexual reproduction, see Schuster (1948b).

32. See Schuster (1958b).

33. *Acrobolbus rhizophyllus* Sharp is a synonym of the Himalayan *A. ciliatus* (Mitt.) Schiffn., see Schuster (1958h); Schuster also demonstrates that this species reproduces asexually by tardily and sporadically caducous leaves, a fact not noted in Sharp (1936). This plant is at once recognizable because of the peculiar, somewhat bluish-green and opaque appearance and because of the flat leaves at maturity developing numerous glistening marginal rhizoids.

34. For a recent account, see Schuster (1954).

35. This species often possesses freely caducous older leaves, much as in the related European *F. fragilifolia;* this fact has not been noted in the recent literature.

36. Schuster (1959) deals with a species of *Cheilolejeunea* closely allied to *C. polyantha* Evs., in which the leaves are tardily caducous, particularly on male plants. *C. polyantha, s. str.,* does not appear to have caducous leaves.

37. For a revision, with keys and illustrations and diagnoses of two new Floridian species, see Schuster (1955a); the name of one of the two described species is changed in Schuster (1956c).

38. A revision, with keys and illustrations, of the North American species in Schuster (1955b, 1956).

39. The genus and the single North American species are described and illustrated in Schuster (1955a). The diagnostic, conspicuous hyaline cells at the lobe apices are not developed on "weak" or juvenile leaves.

40. A revision, with diagnosis of the genus and species, and illustrations, in Schuster (1956).

41. For a modern treatment of the species, see Buch (1936), Müller (1947a) and Schuster (1949, 1953). It it to be noted that *C. portoricense*, a blue oil body species, occurs in the Southeast; this has not been previously reported from North America, but will be dealt with in a revision of the North American species (see Schuster, 1959a).

42. The diagnosis of the gemmae and their assigned position in *Arnellia* (in Frye & Clark, 1937-47) are incorrect.

43. Diagnosis of the genus, keys and illustrations in Schuster (1958b). The two species of *Mylia* are robust, very firm plants; the *Chiloscyphus* is a delicate, translucent plant.

44. Gemmae appear to have been observed only by Howe (1899); see the discussion of this genus in Schuster (1955c). The cushioned purplish areas below the underleaves are absolutely diagnostic of this genus.

45. Arzeni (1948) correctly describes the gemmae of this species. The illustration of the gemmae in Müller (1939-40) is incorrect.

46-49. These taxa dealt with in detail in Schuster (1951a, 1953, 1958e); *Barbilophozia* and *Orthocaulis* are regarded as good genera by some (*i.a.*, Evans, 1935; Buch, Evans & Verdoorn, 1938), but see also Andrews (1948).

50. For useful treatments of the species see Schuster (1949, 1951, 1953, 1956b, 1958d) and Arnell (1950), and the long paper of Müller (1947), all of which reject the species concepts of Douin (1920, 1928) which are followed by Frye & Clark.

Scapania subg. Jensenia Arnell (Arnell, 1956) may key here. The plants of this subgenus lack the keeled leaves typical of *Scapania* but have the unequally bilobed leaves of that genus.

51. For illustrations and keys to species, see Schuster (1951a, 1953); Leiocolea is regarded as a genus by some, although regarded as a subgenus by Müller (1939), who eventually (1951-56) accepted is as a good genus.

52. For keys to species, see Schuster (1951a, 1953); based upon study of one stem of the original, *L. violascens*, placed in Massula, appears to be a synonym of *Lophozia grandiretis*. The subgenus was first described by Müller (1939).

53. *Crossocalyx* is regarded as a genus by Müller (1951-56), following Meylan (1939); Frye & Clark fail to mention the group, but follow the erroneous treatment of Buch (1933) and place the single species in *Isopaches*. Schuster (1951a) suggests that the single species be placed into a subgenus of its own, within *Anastrophyllum*, or within *Eremonotus*. Time has demonstrated that the latter alternative is preferable. It should be pointed out that the generic type of *Sphenolobus* is *E. hellerianus*, since this was the only species placed by Lindberg in his subgenus Sphenolobus. Therefore, if we are to follow the rules of priority to the letter, Crossocalyx is a synonyn of Sphenolobus, and Sphenolobus as currently used is without a name.

54. The single species often referred to an autonomous genus, *Spheno-*

lobus (as in Müller, 1951-56), but a more conservative position is adhered to in Schuster (1951a) who suggests placing Sphenolobus either as a subgenus of *Anastrophyllum* or of *Eremonotus*. The latter course is followed here.

55. Restricted here to *L. bicrenata* (and the European *L. decolorans*); for reasons, see Schuster (1951a) and Andrews (1948). I cannot follow the reasoning of Müller (1951-56) who has finally accepted this as a genus.

56. In the past always referred to as the subgenus "Diplophozia"; the current rules do not allow this usage, so I have returned to the practice of repeating the generic name for the typical subgenus; for keys to species and illustrations see Schuster (1951a, 1952, 1953, 1953a). This subgenus, together with Massula, comprise the genus *Lophozia* of Buch (1933) and Frye and Clark (1946, in 1937-47); for orientation see Schuster (1951a).

57. See Müller (1939, 1942); see Schuster (1951a, 1953) for keys and illustrations.

58. See Schuster (1951, 1951b, 1953) for keys and illustrations of the eastern species; the excellent treatment of Buch (1928) is still standard.

59. See Persson (1949) and annotation 26.

60. *C. doellingeri* has fragile, easily caducous perianths that serve at least as a casual secondary mode of reproduction (Schuster, unpublished). The American species is revised and illustrated in Schuster (1958a). Our species has been found only on the bark of *Sabal palmetto*. *Chonecolea* is a recent segregate from *Clasmatocolea* (Grolle, 1956; Schuster, 1958a).

61. For a revision and illustrations, see Schuster and Blomquist (1955). Arnell (1957) has demonstrated that our single species, heretofore known as *T. nematodes* (G. *ex* Aust.) Howe must be regarded as a synonym of *T. sejuncta* (Ångstr.) S. Arn.

62. The separation of this genus from *Telaranea* is dealt with in Schuster and Blomquist (1955); it should be noted that Müller (1954, 1951-56) incorrectly considers *Microlepidozia* a synonym of *Telaranea* and that Mrs. Hodgson (1956) returns to the old concept that these two taxa are mere subgenera of *Lepidozia*. However, as is evident from her key and discussion, she fails to separate the groups on other than a superficial basis. Certainly branching, as exemplified in the studies of Evans (1912) and Schuster & Blomquist (1955), must be given a primary role in the separation of these taxa. *Microlepidozia* has the unique "*Microlepidozia*-type" of branching; *Telaranea* the "*Frullania-type*" of branching, similar to that in *Lepidozia*. Müller (1939) separated *Microlepidozia* from *Lepidozia* on the basis of lack of oil bodies in the former *vs.* their presence in the latter genus. *Microlepidozia* has oil bodies, at least in the two American species and in the single Japanese species.

63. See Schuster (1955a) for diagnosis and illustrations; we have only the single species *L. cardiocarpa*, confined to the Southeast. The separation of this genus from *Cololejeunea* is arbitrary and perhaps unwarranted.

64. The North American species are revised in Schuster (1955a), who gives a key to the North American, West Indian and Atlantic species; two species new to the United States are described, *A. ephemeroides* and *A. evansii*. Schuster (1956c) shows the latter to be a later homonym of *A. evansii* Herzog from Cuba and proposes the new name *A. cornutissima*. The two regional species are minute, found only in small quantity in central and southern Florida; they are a very pellucid, pure green and bear strongly dimorphic leaves.

65. The North American species revised by Schuster (1955a, 1955b,

1956). See also the monograph of the Indo-Malayan species by Benedix (1953). Our species are usually more yellow- or whitish-green, and more opaque, than the species of *Aphanolejeunea;* most of them do not bear sharply dimorphic leaves.

66. All plants keying to this point are members of the Lejeuneaceae Holostipae; several different keys to these genera are given in Schuster (1954, 1955).

67. In addition to *Porella* and *Ascidiota, Frullania jackii* keys to this point. This species, our only *Frullania* with unlobed, reniform to rotundate underleaves, is found only in unglaciated Alaska, in North America (Schuster & Steere, 1958a). It differs from *Porella* and *Ascidiota* in possessing the "normal" galeate, inflated lobuli typical of the genus, and in the much inferior size (less than 2 mm. wide); the red-brown color is also distinctive.

Ascidiota blepharophylla Massalongo (Nuovo Giorn. Bot. Ital. n.s. 5(2): 255-260, *pl.* 11, 1898) occurs in unglaciated portions of Alaska. The species can be mistaken only for *Porella vernicosa* ssp. *faurieri* (see Ando, 1955; Hara, 1956), which occurs in eastern Asia, eastward to the Aleutian Islands. This latter plant was erroneously reported from Alaska by Frye & Clark (1947, p. 952, in 1937-47) as "*Porella laevigata* var. *killarniensis* Pears." Stephani, and following him all other recent workers, have considered *Ascidiota* as a synonym of *Porella.* I would like to point out that, on the basis of recent concepts of genera in groups like the Lophoziaceae, *Ascidiota* is deemed fully recognizable as a genus. Certainly it is a much more distinctive segregate than *Macvicaria.* The Alaskan plant and its relationships to the Himalayan *A. blepharophylla* are dealt with in detail in Schuster & Steere (1958a).

68. For a treatment of our single species see Schuster (1954); our species is confined to central Florida, while *Brachiolejeunea* is confined to the southern one-eighth of the peninsula.

69. Recently reported, and illustrated, for the United States by Schuster (1954), who discusses the separation of the genus from *Ceratolejeunea.* Only *N. breutellii* is found in the United States; it is known only from coastal Mississippi.

70. In order to perceive this character clearly, several upper leaves must be dissected from the stem, *in toto,* and flattened under the cover glass. The hyaline papilla disappears with age, and so young leaves should be used. See discussion in Schuster (1955). Even on mature lobuli the position of the hyaline papilla is usually indicated by a slight marginal notch.

71. The writer does not regard Euosmolejeunea as more than a subgenus of *Cheilolejeunea,* in which it is included here. The two subgenera are separable as follows:

Lobule at apex with sharp, falcate, elongate apical tooth; underleaves small, narrowed to base, distant; perianths with antical face flat.....Cheilolejeunea
Lobule at apex with a short, blunt, apical tooth; underleaves usually ± large, contiguous to imbricate, rounded to cordate at base; perianths usually with ± distinct dorsal keel.....Euosmolejeunea

This separation is also given in Schuster (1955, p. 120). As is pointed out therein, of the North American species, only *C. decidua* belongs in Cheilolejeunea *s. str.;* all other species, including *C. polyantha* belong in subg. Euosmolejeunea. The basis for such a reorientation of the species will be dealt with at length in a future contribution.

72. In this group of genera the lobules are often vestigial; in this case

the hyaline papilla is situated *at the apex* of the apical tooth. In *Cheilolejeunea* the lobuli are almost invariably well-developed and inflated.

73. In some cases the clavate hyaline papilla is actually inserted at the proximal base of the apical tooth. On older leaves, where the papilla has disappeared, its position is usually marked by a slight notch at the base of the apical tooth *toward the stem*, not toward the sinus.

74. The three American species illustrated and described in detail in Schuster (1956a), with a key to species, a generic discussion and correction of errors in nomenclature in Fulford (1945); these errors were incorporated in Frye & Clark (1937-47).

75. Here taken to include the taxa Microlejeunea and Chaetolejeunea (= Stylolejeunea, *sensu* Evans, 1940), usually accorded generic status; see Schuster (1957). These subgenera are separable as follows:

Lobules various, but usually at least partly inflated, never with a linear apical tooth 4-12 cells long; perianths with antical keel usually sharp.

Stem with medulla of many cell rows; plants medium sized, 600-1500 μ wide; leaves widely spreading (55-85°), with lobules rarely exceeding 0.35 the length of the lobes.....Lejeunea

Stem with medulla of 3 cell rows; plants small or minute, 225-500 μ wide; leaves usually erect or erect-spreading (10-45°), with (in part at least) usually large lobules exceeding 0.4 the length of lobes.....Microlejeunea

Lobules reduced to a small basal fold each bearing a linear apical tooth lying parallel with stem, 4-12 cells long; perianth sharply dorsoventrally compressed.....Chaetolejeunea

A revision of the North American species of subg. Lejeunea has just appeared (Schuster, 1957).

The subg. Chaetolejeunea includes the two species *L. pililoba* and *L. spiniloba* (see Schuster, 1957). This taxon is equivalent to *Stylolejeunea sensu* Evans (1940) and Frye & Clark (1947, in 1937-47), not of Sim. I have examined material of both species assigned to *Stylolejeunea* by Sim; they are indubitably typical species of *Rectolejeunea*, both possessing, *i.a.*, caducous leaves. Therefore, *Stylolejeunea* is a clear synonym of *Rectolejeunea*.

The separation of *Rectolejeunea* from *Lejeunea* subg. Lejeunea is often very difficult. In couplet 28 the former is separated from the latter on the basis of the presence of caducous leaves. *R. phyllobola* often does not develop such leaves, and would then be sought under *Lejeunea*. It and all other species of *Rectolejeunea* differ from all our species of *Lejeunea* subg. Lejeunea in the small cells (marginal leaf cells usually 10-15 μ *vs.* 17-24 μ in *Lejeunea s. str.*). The species of *Rectolejeunea* also frequently possess underleaves whose sides are unidentate or angulate; such underleaves, in the genus *Lejeunea s. lato*, occur only in *L.* (*Microlejeunea*) *laetevirens*, which is quite distinct in the suberect leaves and whitish color.

The separation of *Taxilejeunea* from *Lejeunea* is also very difficult. The traditionally cited difference in orientation of gynoecia (those of *Lejeunea* supposedly occurring singly; those of *Taxilejeunea* forming cymose series, juxtaposed along one side of what appears to be a continuous stem) does not hold regionally, since our *Taxilejeuneae* often have only one or two juxtaposed gynoecia. *Lejeuneae* do not turn red-brown in drying; one of our species of *Taxilejeunea* from southern Florida does. Otherwise it can hardly be separated when sterile from *Lejeunea*. There is also an undescribed species of *Taxilejeunea* (so far known only from Tennessee) which

has the 5-carinate perianths of *Lejeunea*, to which it keys in couplet 30. The occasionally cymosely clustered gynoecia, the marked intermediate thickenings of the cell walls, and the homogeneous, glistening oil bodies characterize this taxon. As I have pointed out (Schuster, 1957) a good case can be made in favor of considering *Taxilejeunea* as a mere subgenus of *Lejeunea*.

76. There is much doubt in my mind whether it will be possible to maintain *Hygrolejeunea* as more than a subgenus of *Lejeunea*, for several reasons: (a) many species of *Hygrolejeunea* have only one subfloral innovation, while the Appalachian race of *Lejeunea lamacerina* commonly has two innovations (Schuster, 1957); (b) the difference in size is, *per se*, meaningless as a generic character, as is the usual greater flaccidity of *Hygrolejeunea;* (c) the larger underleaves of *Hygrolejeunea* represent an accentuation of a feature also evident in such species as *Lejeunea flava*. The concept of *Hygrolejeunea* as a genus may be a mere artifact, based on these species of *Lejeunea* with relatively large underleaves and with a more delicate texture than usual. The genus has not been previously reported for North America but is represented in the unglaciated portions of Alaska by *H. alaskana* Schuster & Steere *ms.* (1958).

77. See Schuster (1956) for diagnosis and treatment of the North American species *D. rudolphiana*.

78. A review of the North American species recently appeared (Schuster, 1957c), in which it is demonstrated that our two species (*H. tenuis, H. hutchinsiae*) are both synonyms of *H. sakuraii*.

79. The single species, *D. ovata*, is incorrectly reported for Newfoundland and Wisconsin in Frye & Clark.

80. For a key to the subgenera (Kaalaasia, Scapaniella, Buchiella, Scapania or "Euscapania") see Schuster (1953, pp. 430-431). It is to be noted that *Scapaniella* Buch, accepted as a genus in Frye & Clark (*l.c.*) is not accepted here, it is also denied generic rank by Müller (1944, 1951-56). Schuster (1951, 1953) gives detailed notes on many species; see also the classical paper by Buch (1928); Müller (1951-56) reviews almost all of our species.

Arnell (1956) has recently segregated *Scapania lapponica* into a new subgenus, Jensenia, which is characterized by the essentially unkeeled leaves. The species of this subgenus can easily be mistaken for *Lophozia* or *Sphenolobus;* they differ in having elliptical, smooth gemmae, and in facies. A single species of Jensenia, identical to *S. lapponica* or very closely allied to it, was collected by the writer in northern Ellesmere Island. This plant will be discussed and illustrated in another connection.

81. Recognized first as a genus, *Macrodiplophyllum* (Buch) Perss. (1949). I am of the opinion that its three species (*M. plicatum, microdontum, imbricatum*), all found in northwestern North America, could well have been retained within *Diplophyllum* as a subgenus, as originally done by Buch (1928).

82. *Lophochaete* Schuster (see Schuster, 1957c). Based on *Lepicolea fryci* Perss., a species not exhibiting direct affinities to *Lepicolea*, differing, *i.a.*, in the smooth, "free" perianth. *Lophochaete* is most closely allied to *Temnoma s. str.* (see annotations 83-87).

83-87. Keys to species, illustrations and discussions of these taxa in Schuster (1951a, 1953). *Tritomaria* is revised in Schuster (1958e), with addition of a new species. *Orthocaulis* is often given the rank of a genus.

Our only species of *Chandonanthus* is *C. setiformis*. This species has generally been known, in North America, as "*Temnoma*" *setiforme*, after Howe (Evans, 1935; Frye & Clark, 1937-1947; Schuster, 1951, 1951a). *C. setiformis*, however, is not related to *Temnoma*. This latter genus has a trigonous perianth; the rhizoids restricted to fascicles at the underleaf bases; elongated and essentially non-collenchymatous leaf cells; a 1:1 spore-elater diameter ratio; the epidermal cells of the capsule wall pellucid and colorless and devoid of thickenings (except in the cell-rows immediately adjacent to the sutures of the valves). In all of these features *Temnoma*, as exemplified by the generic type (*T. pulchella*), differs from *Chandonanthus;* the critical distinguishing features of *Temnoma s. str.* have recently been discussed by Schuster (1957c, 1958c). *C. setiformis* does not possess a single one of the critical generic criteria outlined for *Temnoma*. This species is best regarded as an isolated species within the genus *Chandonanthus*, perhaps deserving subgeneric segregation. In my opinion *Temnoma s. str.* belongs unquestionably to the suborder Ptilidiinae, within the Blepharostomaceae. *Chandonanthus* possesses the scattered rhizoid initials of the Jungermanninae and represents a primitive genus of the Lophoziaceae. Recent treatments, as exemplified by Buch (1933) and Evans (1939), placing *Temnoma* in the Lophoziaceae cannot be followed.

88-89. *Eremonotus* (with *E.* [Crossocalyx] *hellerianus* = "*Isopaches*" *hellerianus* [Buch, 1933; Frye & Clark, 1946, in 1937-47] and *E. minutus* = *Sphenolobus minutus*) could readily be interpreted as congeneric with *Anastrophyllum;* both of these alternative treatments are discussed in Schuster (1951a). *Anastrophyllum* is understood to include *A.* (Eurylobus) *hellerianus*, following Schuster (1951a); Müller (1951-56) considers Eurylobus a subgenus of "*Sphenolobus*" (*Eremonotus*). Müller (1947, 1954) accepts *Crossocalyx* as a monotypic genus for *E. hellerianus;* but see discussion in annotation 53. The high arctic *Scapania* subg. Jensenia S. Arn. may key here.

90. See the various recent treatments by Müller (1947), Schuster (1949, 1953, 1956b) and Arnell (1950), all of which stand at variance to the species-fragmentation in Douin (1920, 1928) as copied by Frye & Clark (*l.c.*). See annotation 99 for a key to the subgenera of *Cephaloziella* here accepted.

91. For the new species, *M. paroica*, see Schuster (1957b); for a valuable discussion of the separation of *Marsupella* and *Gymnomitrium* see Müller (1942, 1951-56), who separates the two genera on the basis of vegetative differences, in a manner other than the traditional (as, *i.a.*, in Frye & Clark, 1943, in 1937-47).

92. *Dianthelia steerei* Schuster (1949a) is perhaps better regarded as a species of *Gymnomitrium*, *G. steerei* (Schust.) Schust. *Gymnomitrium elgonense* Arnell (1956a) from the Ruwenzori Mts. of Africa is evidently identical; Arnell (*in lit.*) states he can find no differences between them.

94. *Nardia lescurii* and *N. insecta*, stout fleshy plants with lanceolate to subulate underleaves, may be mistaken for *Harpanthus*. The latter has much smaller leaf cells, with numerous, smaller oil bodies; it possesses a slender, not fleshy stem and has the sexual branches postical in origin. In *Nardia* the gynoecia and androecia are on leading leafy shoots not of postical origin and the cells each have only 2-4(5) very large oil bodies.

95. For illustrations see Schuster (1951a); the position assigned this genus in Frye & Clark (*l.c.*) is erroneous.

96. Often considered a discrete genus; for keys to species, and illustrations, see Schuster (1951a, 1953).

97. The extraordinarily polymorphous genus *Plagiochila* dealt with in detail in Schuster (1957a, 1958b). However deviant, the species can usually be recognized as belonging to *Plagiochila* by the dorsal leaf margin being deflexed at least near the base and also by the absence of gemmae.

98. *Barbilophozia* and *Orthocaulis* are regarded as independent genera by some, united to form the genus *Barbilophozia* by Müller (1951-56), and considered congeneric with *Lophozia* by most older workers and by Schuster (1951a, 1953).

99. Several of our species of *Cephaloziella* have obliquely inserted leaves (*C. obliqua, C. rappii, C. rhizantha, C. hyalina*); see Schuster (1956b) for a discussion of these and figures of *C. rhizantha*, as well as the synonymy of *C. ludoviciana* and *C. floridae*.

Cephaloziella is here taken to include Prionolobus as a subgenus, as well as Dichiton and Cephaloziopsis. These subgenera are separable as follows:

Branching exclusively or predominantly postical and intercalary; usually freely developing gemmae.

Leaf margins entire, except for lobing, only rarely with 1-2 subbasal teeth.

Perianth mouth with cells strongly elongated (2-8:1); gemmae smooth, ellipsoidal. ..... Cephaloziella

Perianth mouth with cells nearly isodiametric (1-2:1); gemmae papillate. ..... Dichiton

Leaf margins clearly dentate; gemmae polygonal; perianth mouth with cells strongly elongated..... Prionolobus

Branching partly or largely terminal, the branches furcate; without gemmae; leaf margins entire..... Cephaloziopsis

All the species except three belong to *Cephaloziella* s. str. The only record of Dichiton in North America (Frye & Clark, 1944, in 1937-47), based on *D. calyculatum*, is erroneous. As pointed out by Schuster (1956b), *Cephaloziella rhizantha* (Mont.) Schust. (= *C. ludoviciana* and *C. floridae* of Frye & Clark) may represent a species of Dichiton. Prionolobus (with *P. tuneri*) occurs only on the west coast. Cephaloziopsis, previously known from the British Isles and Norway, is reported for the Appalachian Mountains by Schuster (1958d), who attributes *C. pearsoni* to this area.

100. This high-altitude (4500-6800 ft.) species of the Southern Appalachians is illustrated and described in detail in Schuster (1958b).

101. See treatment in Schuster (1958a), and differentiation from *Cephaloziella* in Schuster (1956b).

102. *Lophozia* (Leiocolea) *badensis*, a small, underleaf-free species, also keys here. It is distinctive in the tubular perianths, which are sharply constricted into a short but distinct beak, and in the few but large (2-5 per cell) oil bodies. Both criteria separate it and other species of Leiocolea from other subgenera of *Lophozia*. For treatment of the subgenera, see Schuster (1951a, 1953); the latter gives most of the North American species; see also annotations 52, 55, 56.

103-104. For figures and discussion see Schuster (1951, 1953). Arnell (1956) makes a new genus *Obtusifolium* out of *L. obtusa*.

105. For figures, generic and specific diagnoses and keys, see Schuster (1958b). The two species (*M. anomala* and *M. taylori*) are distinct because of their coarseness, firmness, and the postical mat of dense rhizoids.

106. For figures and discussion see Schuster (1955c).

107. *Anomylia* Schuster, for "*Mylia*" *cuneifolia* of authors; see Schuster (1958b).

108. Southeastern forms of *L. heterophylla* and an undescribed, entire-leaved species of *Lophocolea* from the Southern Appalachians may key here; these are members of a genus in which the leaves are normally bilobed. For a revision of the species of the genus *Chiloscyphus* see Müller (1942a).

109-110. For a revision, keys, diagnosis and plates, see Schuster (1958b). Almost all American reports of *Pedinophyllum* refer to entire-leaved forms of *Plagiochila asplenioides*, from which it must be separated with great care, *e.g.*, by the lack of a differentiated cortex. *Pedinophyllum* is very rare in North America, appearing confined to limestone areas from Mass. to Conn. west to Ohio.

111. For diagnosis and illustrations, see Schuster (1953).

112. Including only *J. lanceolata*, as in Schuster (1953); Müller (1951-56) also thus restricts *Jungermannia;* the other species assigned here in Frye & Clark more properly belong in *Solenostoma* (including *Plectocolea*).

113. Accepted in the broad sense of Mitten to include Plectocolea as a subgenus. For the reasons that such a broad circumscription is preferable, see Schuster (1953), who gives a key to the subgenera and most of the species.

114. See also the Artificial Key to Genera.

115. After some deliberation I have followed the spelling of Joergensen (1934, p. 49) who states the genus is named "efter Mørk [Moerk]." This, then represents a correction in spelling of the original generic name *Moerckia* of Gottsche. Joergensen adds: "Lennis skrives navnet 'Moerk' (sannsynligivis Mørk); c'en synes å skyldes 'latinisering.' (Sammenlign Nomenklaturreglene Art. 25 Recommendations IV c)." My previous usage of *Moerkia* (Schuster, 1949, 1953) is thus not an error in spelling, as Steere (1954) alleges.

116. The genus *Trichostylium* is here used for three species previously placed in *Riccardia*, **Trichostylium pinguis** (L.) comb. nov. *Jungermannia pinguis* L., Sp. Pl. ed. 1: 1136, 1753; *Riccardia pinguis* S. F. Gray, Nat. Arr. Brit. Pl. 1: 684, 1821) and **Trichostylium pellioides** (Horikawa) comb. nov. (*Riccardia pellioides* Horikawa, Bot. Mag. Tokyo 51: 429, 1937), and **Trichostylium lobata** (Schiffn.) comb. nov. *Ricardia lobata* Schiffn., Kais. Akad. Wiss. Wien 67: 178 1899. Mitzutani & Hattori (1957) have used *Trichostylium* as a subgenus of *Riccardia*, but it undoubtedly represents a good genus. In manuscript I had assigned these two taxa to a new genus, for the reason that *Trichostylium affine* Corda, the type of the genus, is unquestionably a mixture of female "*Riccardia pinguis*" and a male plant of some other family. Hence the genus can be recognized only if we arbitrarily base it on the female plants. Since the name has been recently revived, perhaps injudiciously, even if only on a subgeneric level, I propose that it be maintained; it has not been used for over 120 years. The anatomical and cytological bases for the separation of the genus will be analyzed in another connection (Schuster, 1958f).

117. In addition to the three "old" and well-known species of *Pellia*, *P. epiphylla*, *neesiana* and *fabbroniana*, a fourth species was recently described by Krajina & Brayshaw (1951).

118. From a study of a few preserved plants sent to me by Dr. J. Proskauer, I would conclude that *Geothallus* Campbell (Bot. Gaz. 21: 13, 1896), with the single species *G. tuberosus*, is not generically distinct from

Sphaerocarpus, leading to the combination **Sphae ocarpus tuberosus** (Camph.) comb. nov. (*Geothallus tuberosus* Campbell, Bot. Gaz. 21: 13. 1896).

119. Müller (1951-1956, pp. 320-321) divides the suborder Marchantiinae into the "Subordo Caudiciformis" and the "Subordo Quadranticae," based on the nature of the initial divisions the zygote undergoes. (Müller incorrectly states "Eizelle.") This arrangement cannot be followed for two reasons. Firstly, it is impossible on nomenclatural grounds to divide one suborder into two others. Secondly, it has been shown repeatedly that there is wide variation, *e.g.*, in *Riccia*, from one species to the next, and sometimes within the species, in the orientation of the walls formed *after* the initial transverse division of the embryo. Certainly a "quadrant" type of embryo appears to have evolved a number of times from the presumably more primitive "filamentous" type.

120. Except in the isolated genus *Bucegia*, in which the air chambers are without filaments and lie at least locally in two layers.

121. *Oxymitra* is separated into a unigeneric family, Oxymitraceae by Müller (1939-40). In the writer's estimate, this genus can readily be retained within the Ricciaceae.

See McGregor (1955) for valuable notes on the Ricciaceae and Müller (1941) for a treatment of the difficult *Riccia fluitans* complex. Schuster (1953) gives keys to most species, and to those of the *R. fluitans* complex.

122. Shimizu & Hattori (1953-55) demonstrate that *Clevea* (not *Cleva!*) is congeneric with the older *Athalamia* Falconer.

123-124. For careful illustrations and good diagnoses see Shimizu & Hattori (*l.c.*).

125. Schuster (1953) illustrates the American species, with the exception of *M. californica*. It should also be pointed out here that the discussion of the thallus anatomy of *M. californica* by Preston (1939) is totally incorrect, evidently being based on the erroneous identification of *Targionia hypophylla* for *Mannia*. The evidence for this, together with a detailed summary of *Mannia californica* and a corrected diagnosis, are given in Schuster (1958g).

126. Shimizu & Hattori (1953-55) regard *Cryptomitrium* as a subgenus of *Mannia*, a treatment which may prove correct. However, they are certainly incorrect in considering *Neesiella* (founded on *Grimaldia* rupestris) as a section of *Cryptomitrium*. I consider *Neesiella* here to be generically identical with *Mannia*, however narrowly or broadly we may wish to restrict that genus. It cannot be placed in *Cryptomitrium*. The artificiality of such an attempted disposition is clear from the fact that *Mannia pilosa* is placed by Shimizu & Hattori in *Cryptomitrium* sect. Neesiella, while the doubtfully specifically distinct *M. sibirica* is placed in the subgenus Mannia. I have elsewhere (Schuster, 1956d) commented on the artificiality of such an orientation of taxa. Arnell (1956) regards *M. sibirica* as a mere variety of *M. pilosa!*

127. See McGregor (1955) for notes on many of our species and specifically as to the synonymy of the recently described species of *Riccia* of Jacobs (1949).

128. Terrestrial phases of *Ricciocarpus* are often mistaken for *Riccia* and other genera of Marchantiales. Such forms have a persistent, narrow, conspicuous dorsal groove or furrow, are bright yellow-green and have an epidermis with distinct, if undifferentiated pores and oil cells (see Schuster, 1953, for figure).

129. Established for the yellow-spored species of *Anthoceros*, *i.e.*, *A. laevis*, *A. donellii*, etc.; see Proskauer (1951), Schuster (1953). It should

be noted that Meijer (1954) refuses to accept the validity of *Phacoceros*, stating "it is not necessary to accept two separate genera" for the yellow- and black-spored species. Under any conditions, *Phacoceros* is at least worthy of subgeneric rank.

130. Proskauer (1948) gives valuable notes on several of our species. Schuster (1953) discusses the northern species; Schuster & Bryan (1958) discuss *A. megalosporus* G. (= *A. ravenellii* Aust.) in detail. It should also be noted that Schuster (unpublished) has also found two other species of *Anthoceros s. str.* in the Southeast, one of which is the European *A. husnoti* Steph., which is probably only a race of *A. punctatus*, and also a tropical species not previously found in North America. As a consequence, the taxonomy of our species is wholly fluid and in need of thorough study. Frye & Clark's treatment (1937-47) of the group, especially with regard to the eastern and western representatives of the black-spored species, is wholly unacceptable. *A. carolinianus*, which they accept as a species, is not specifically distinct from *A. laevis*, although Proskauer (1951) recognizes it as *Phacoceros carolinianus* (Mx.) Prosk.; this was first definitely stated by Schuster (1953), who reduced it to a form of *P. laevis*. Frye & Clark made two serious errors with respect to *A. meridionalis* and *A. reticulatus*. They "key" the first under the yellow-spored species, yet the type of *A. meridionalis* is black-spored, and represents a species allied to *A. punctatus*, although without the spines arising from a reticulum. *A reticulatus* is considered by them a simple synonym of *A. meridionalis*, yet it does not even belong to the same genus, being a simple synonym of *Phacoceros laevis carolinianus*, as is evident from study of the type. Also Frye & Clark erroneously cite *A. fusiformis* as a simple synonym of *A. punctatus*.

131. Müller (1939-40) has placed this genus in the monotypic family Notothylaceae. I regard *Notothylas* as merely a strongly reduced genus of the Anthocerotaceae.

132. The outline classification is based largely on Schuster (1953), with the following significant changes: (1) The Radulinae are recognized as a suborder discrete from the Porellinae; (2) the Marchantiales are split into four suborders, rather than the two customarily recognized. A few recent generic synonyms are included in brackets, and subgeneric groups here recognized within more inclusive genera, but often recognized by others as separate genera, are cited within brackets, in roman type. North American genera *only* are listed.

133. The subordinal classification is largely after Schuster (1953). I have organized the numerous families of Jungermanninae into three series, each formed of families with rather distinct affinities. These series remain nameless for the time being, since their formal recognition must follow more careful study of the exotic genera.

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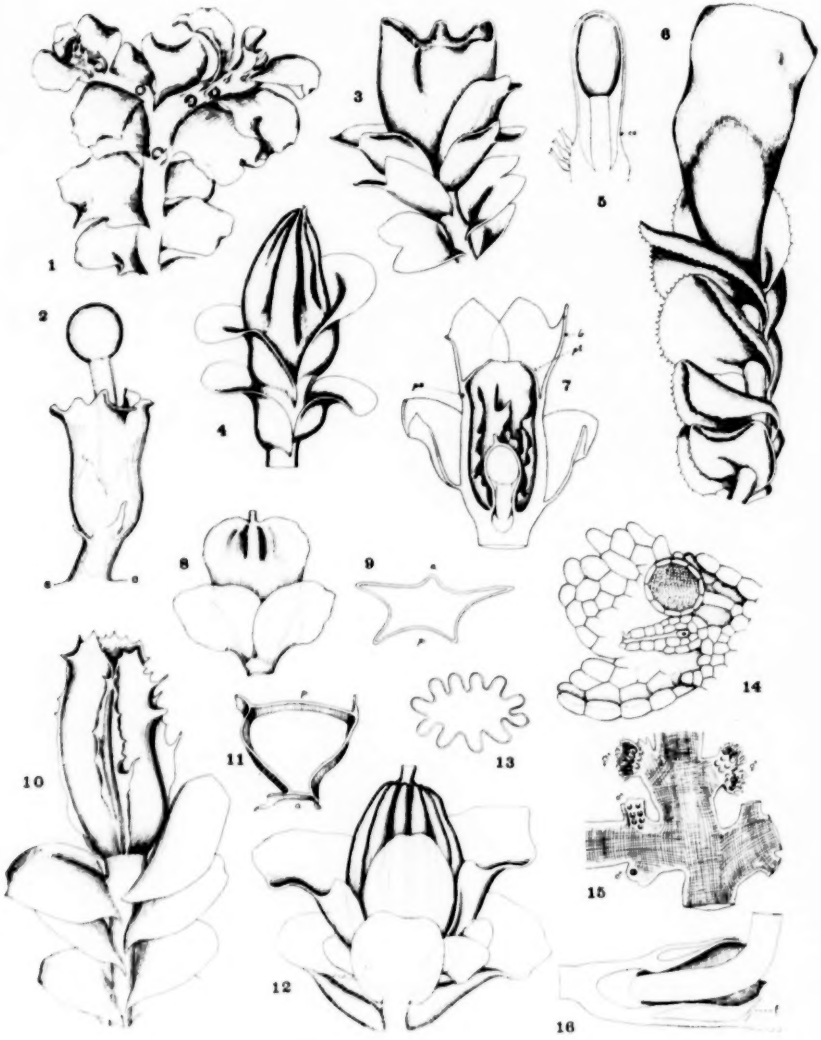
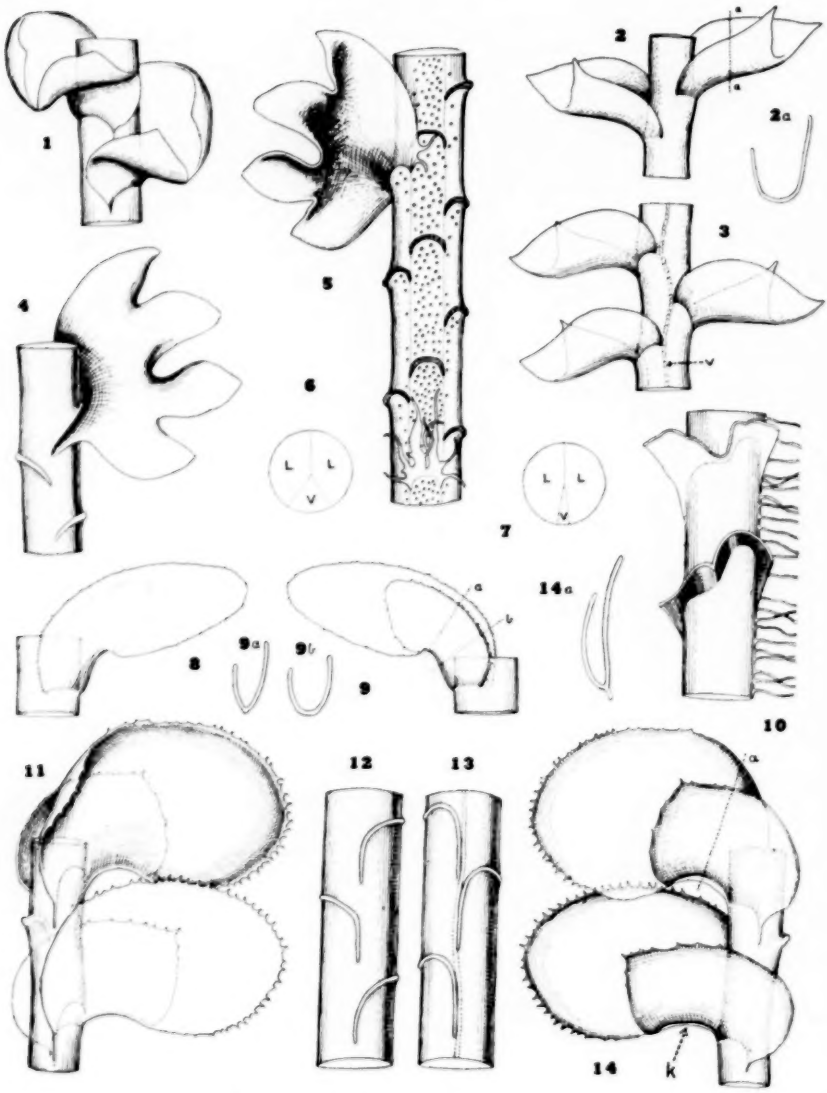


FIG. 1. Illustrations of key characters

FIG. 2. Illustrations of key characters.



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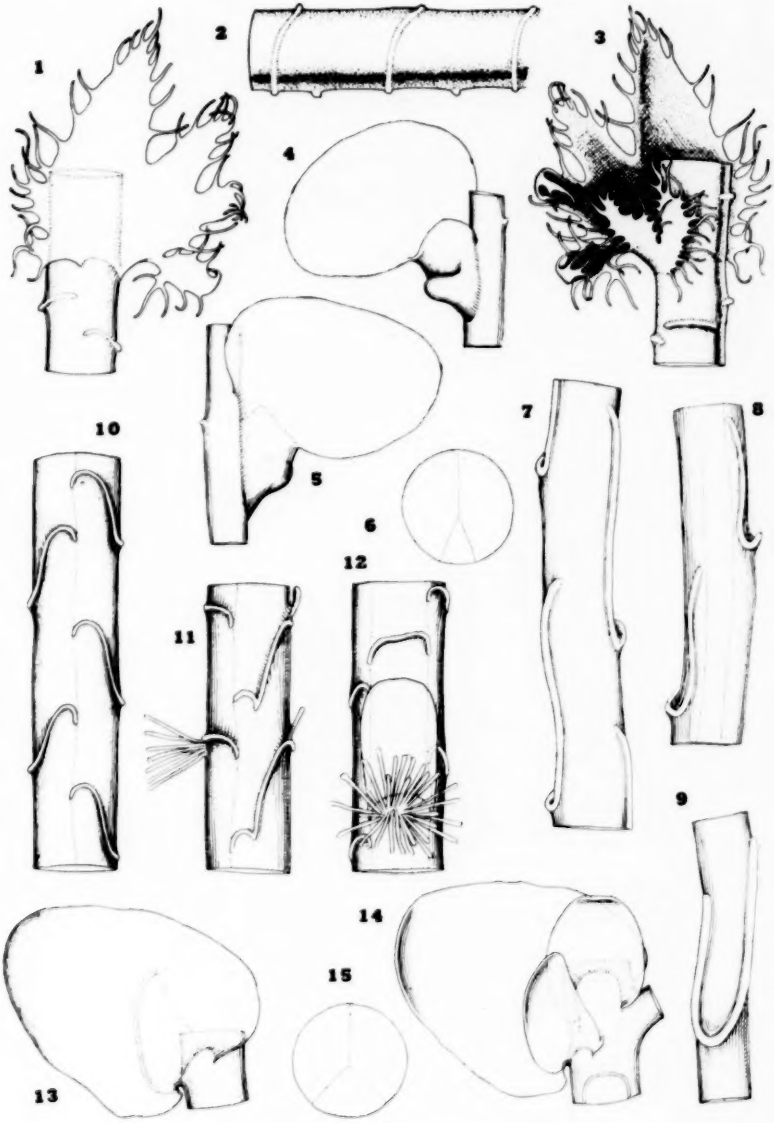

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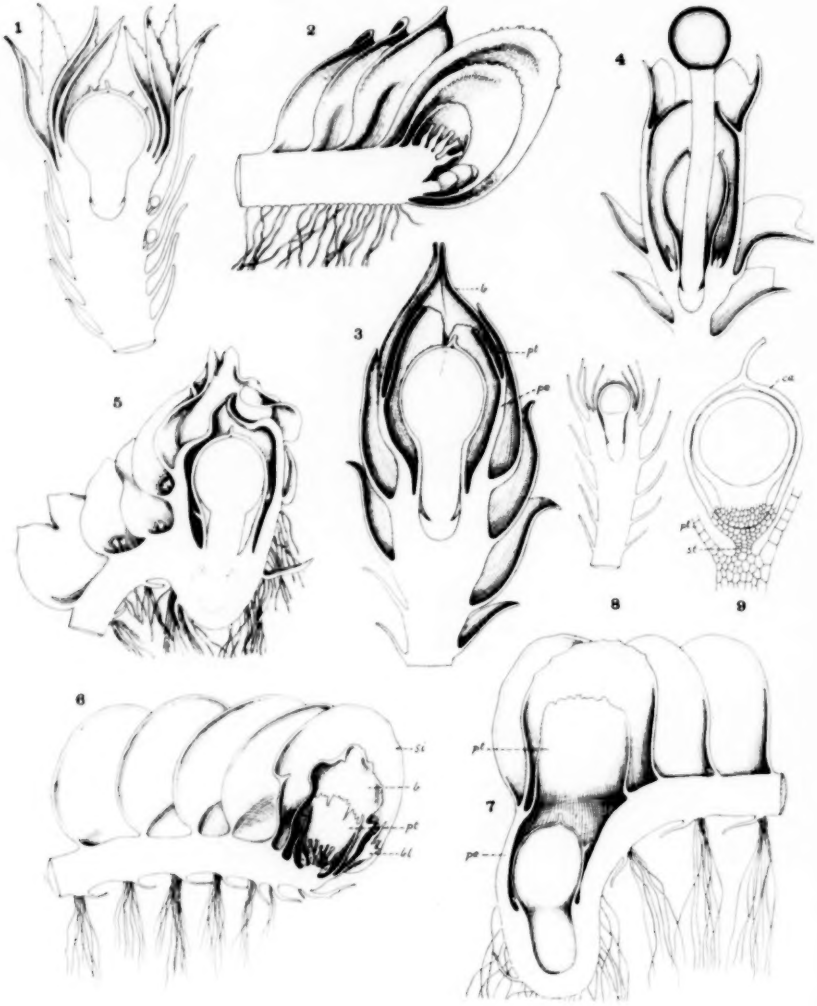

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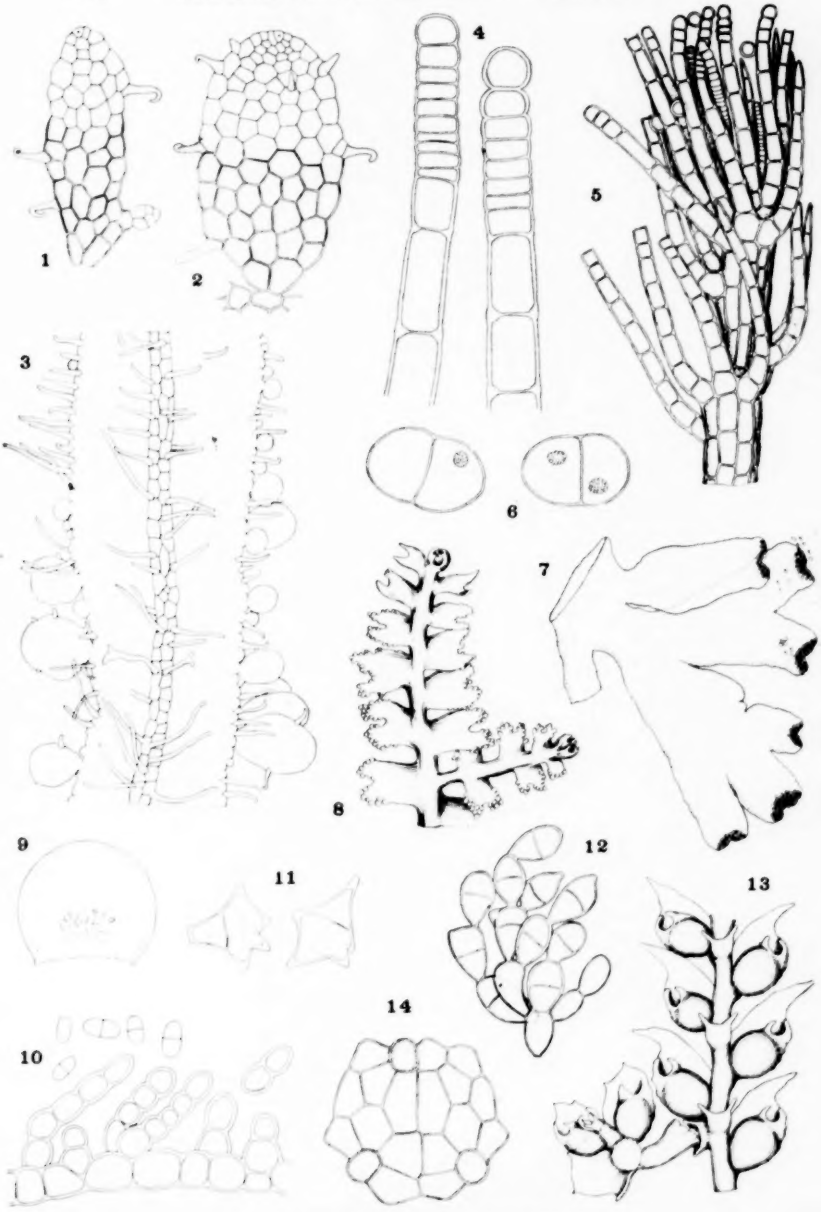

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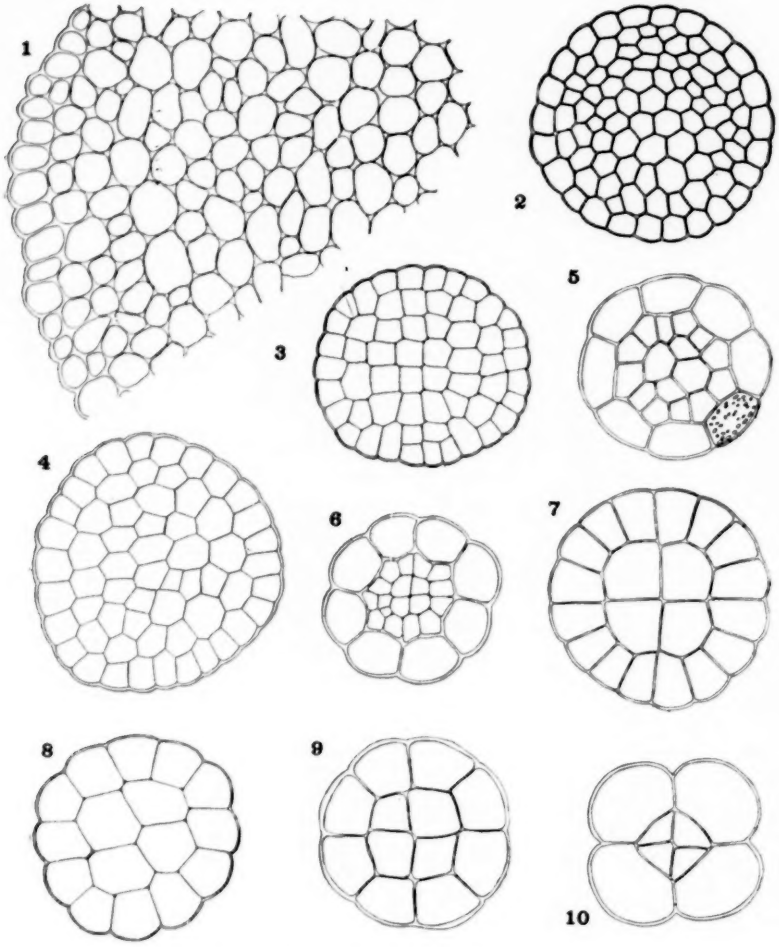

FIG. 7. Illustrations of key characters.

FRULLANNIA GYMNOTIS FOUND IN THE UNITED STATES

LOIS CLARK[1]

Frullania gymnotis Nees & Mont. was described from Leprieur's Nos. 360 and 366, collected in "Guiana" (Montagne, 1843, p. 257). It is not uncommon south of the United States border. We have seen material from Jamaica, Guadeloupe, Venezuela, Galapagos Islands, Cocos Island, Panama, Costa Rica, Nicaragua and Honduras. It is also reported from Surinam and eastern Brazil, but we know of no report from Mexico or Guatemala. We now have it from three widely separated localities in the southern United States, as follows:

SOUTH CAROLINA, Charleston Co., about 3 mi. S. and 1 mi. E. of Awendaw, about 33° 3′ N, 79° 33′ W, on bark of *Liquidambar styraciflua*, *W. T. Batson*, Dec. 21, 1956. FLORIDA, Columbia Co., 6 mi. NW. of Fort White, at Chatucknee Springs, on trunk of tree, *L. F. Koch* 7215, Sept. 4, 1954. LOUISIANA, St. Martin Parish, Bayou Chene, about 30° 9′ N, 91° 30′ W, *Arthur Svihla* 344, Dec. 5, 1926, determined by Howe as *F. obcordata*, and so reported (Svihla, 1939). The female inflorescence, however, leaves no doubt that it is *F. gymnotis*.

The chief distinctions between *F. gymnotis* and *F. obcordata* lie in the female inflorescence. In the former the margins of the bracts and bracteoles are sinuous to dentate, while in the latter they are entire. Sterile material is more likely to be confusing, but *F. gymnotis* usually has a number of short, somewhat microphyllous branches near the tips of the branches. These short branches usually do not extend beyond the leaves of the branch from which they arise. Also the saccate ventral lobes of these microphyllous branches are sometimes mammillose. In *F. obcordata* neither such microphyllous branches nor any mammiliosity has been observed.

Our drawing of the stylus of *F. gymnotis* (Clark & Svihla, 1948, *fig.* 3) is misleading in that it illustrates a young one. When mature the stylus is two or more cells wide at base and distinctly triangular in form.

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REVIEW OF THE GENUS HOMALIADELPHUS[1]

ZENNOSKE IWATSUKI[2]

The genus now known as *Homaliadelphus* was first split from *Homalia* by Dixon and Potier de la Varde as *Homaliopsis* in 1928. They included in it only one species, *H. targionianus*, known from India, China (Yunnan) and Japan. (They attributed the basionym to Gough, but *Homalia targioniana* Gough was merely a manuscript name which was validated by Mitten's description, under *Neckera*, in 1859.) Since *Homaliopsis* proved to be a later homonym, Dixon and Potier de la Varde later (1931) proposed the name *Homaliadelphus* as a replacement. They emphasized the pilose calyptra and smooth, simple peristome teeth as the main characters distinguishing the genus from *Homalia*. Later Noguchi (1950) reported linear, fragile, inner peristome teeth. The genus is more clearly distinguished, however, by having small lobes at the adaxial base of each leaf similar to those found in some hepatics. The leaves are complanate-foliate in four rows with lobes attached to the adaxial surfaces (*fig.* 47).

Brotherus (1899) reported *Homalia targionianus* from Japan, and Okamura (1915) described a new Japanese species as *H. laevidentata;* this was reduced by Dixon and Potier de la Varde (1928) to a synonym of *H. targionianus*. Noguchi (1950), on re-examining *Homalia laevidentata*, made the combination, *H. targionianus* var. *laevidentatus*, and also described *H. targionianus* var. *rotundatus*.

In the United States, Williams (1931) described a new species of *Homalia*, *H. sharpii*, from Tennessee, based on Sharp's collections and discussed its relationship to *H. targionianus*. Grout (1934) said, "The discovery of this near relative of Asiatic species is one of the most interesting of recent bryological discoveries in North America." This species was reported by Patterson (1944) from Virginia and by Wagner (1951) and Crum (1951) from Mexico. However, *H. targionianus* var. *rotundatus*, of Japan and Formosa, is almost the same as *H. sharpii*. After careful examination of the type specimens of the two taxa, I propose to combine var. *rotundatus* with *H. sharpii* instead of *H. targionianus* (details are discussed later).

Specimens were made available through the courtesy of Dr. D. D. Keck of the New York Botanical Garden (NY) and Dr. H. A. Crum of the

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 185, and from the Hattori Botanical Laboratory, Japan.

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National Museum of Canada (CAN). I am also indebted to Dr. A. Noguchi and Dr. S. Hattori of Hattori Botanical Laboratory (NICH) for their many criticisms and for specimens and to Dr. A. J. Sharp and Mr. H. Sherman of the University of Tennessee for their suggestions.

KEY TO SPECIES AND VARIETIES OF HOMALIADELPHUS

1. Female buds about 1.5-2.5 mm. long; perichaetial leaves narrowly lingulate from a sheathing base, apex round and crenate; primary stem sparsely and irregularly branched, secondary stems about 1.5-2.5 mm. wide with leaves 2

1. Female buds about 0.7-1.5 mm. long; perichaetial leaves mostly broadly oblong or spatulate, irregularly serrate at apex; primary stems densely and somewhat regularly branched, secondary stems 1.0-2.0 mm. wide with leaves 3

2. Dioicous. Setae 4-7 mm. long; capsules 1.7-2.2 mm. long; leaves of median parts of secondary stems averaging 1.3-1.5 mm. long, 1.0-1.1 mm. wide ..... 1. *Homaliadelphus targionianus*

2. Phyllodioicous. Setae 1.5-3.0 mm. long; capsules 1.0-1.7 mm. long; leaves of median parts of secondary stems averaging 1.0-1.1 mm. long, 0.75-0.85 mm. wide ..... 2. *Homaliadelphus laevidentatus*

3. Leaves mostly ovate, 1.3-1.5 times as long as wide; leaf margins essentially straight where lobes are attached ..... 3a. *Homaliadelphus sharpii* var. *sharpii*

3. Leaves mostly rotundate, 1.1-1.3 times as long as wide; leaf margins strongly curved where lobes are attached ..... 3b. *Homaliadelphus sharpii* var. *rotundatus*

1. HOMALIADELPHUS TARGIONIANUS (Mitt.) Dix. & P. de la Varde, Rev. Bryol. et Lichénol. 4: 142. 1931. *Omalia* [Homalia] *targioniana* Gough, *ms. Neckera targioniana* Mitt., Jour. Proc. Linn. Soc. London, Bot. Suppl. 1: 117. 1859. *Homalia levieri* C.M., Nuov. Giorn. Bot. Ital. 4: 263. 1897. *Homaliopsis targionianus* (Gough) Dix. & P. de la Varde, Ann. Bryol. 1: 48. 1928.

Plant loosely to densely matted, shining green above, yellowish to brownish below. Primary stems slender, prostrate, irregularly branching, bearing brown radicles; secondary stems slender, reaching 2.0 cm. in length, often short, prostrate or somewhat erect, mostly 2.0-2.5 mm. wide with leaves; cross-sections of stems elliptic, composed of 5-6 outer layers of thick-walled cells and an inner core of hyaline, thin-walled cells, without a central strand; apex of branches obtuse, leaves complanate-foliate in four rows, two rows on each side, broadly ovate to rotundate from a narrow base, entire, mostly asymmetric, 1.35-1.6 mm. long, 1.0-1.1 mm. wide, smaller at the base and tip of secondary stems, larger in the middle; distal part of extreme leaf base becoming incurved or bearing semicircular, entire, small lobes toward the inside (*fig.* 32-47) between the two closely appressed rows of leaves; cells at margin and leaf tip small, rectangular to quadrate, with thick walls and rounded

corners, (5)6.5-10 μ long, 7.5-10 μ wide, those toward the center rhombic, 15-25 μ long, 6-10 μ wide, with slightly pitted walls, those of the inner basal part elongate, 20-60 μ long, 6-12 μ wide, with pitted walls, those on the margins of lobes small, rectangular to rhombic, 5-10 μ long, 5-8.5 μ wide.

Inflorescence dioicous; female buds in axils of leaves, erect from the prostrate stem (*fig.* 47), about 1.5-2.5 mm. long including perichaetial leaves; outer perichaetial leaves short, inner longer, narrowly lingulate from the sheathing base, widest near apex, almost entire to crenulate at the roundly obtuse apex, 0.35-0.48 mm. wide near apices, about 1.5 mm. long; cells of apical portion quadrate to rhombic, 10-22 μ long, 6-9 μ wide, toward the base elongate, 35-80 μ long, 6-9 μ wide. Setae 4-6 mm. long, about 0.15 mm. in diameter, smooth, brown; capsules erect, oblong-cylindric, neck distinct, 1.7-2.2 mm. long, 0.55-0.7 mm. wide, brown; outer peristome teeth lanceolate, pale yellow, smooth to indistinctly striate at base, about 0.15 mm. long; endostome membrane low, segments linear, fragile, often adherent to the exostome; spores globose, minutely papillose, 15-20 μ in diameter; operculum obliquely rostrate from a conical base. Calyptra cucullate, 1.7-1.9 mm. long, sparsely pilose.

Male plants similar to female plants in size, with perigonia gemmiform, in axils of leaves; outer perigonial leaves oblong-spatulate, obtuse to round at tip, with a broader base, about 0.55-0.75 mm. long; innermost perigonial leaves ovate-apiculate, 0.3-0.6 mm. long; antheridia few, about 0.18 mm. long; paraphyses few.

SUBSTRATES: Usually calcareous rocks in Japan and trees and rocks in India.

SPECIMENS EXAMINED: INDIA: Nilghiri, *Gough* 710 (holotype, NY). Pollong, *Griffith* 444 (NY). Beddome, *Griffith* 304 (NY). Mahussov et Fagoo, *Griffith 2* (NY). Palni Hills, 3400 ft., *G. Forean* 1551 (CAN). JAPAN: SAITAMA PREF. Mt. Buko, *ca.* 1000 m. alt., *K. Sakurai* (*Musci Selecti et Critici* 24). Mt. Buko, *ca.* 900 m., *U. Mizushima*, 7945 (TENN). Kagemori, *ca.* 300 m., *S. Hattori* (*Musci Japonici* 272). Same locality, *A. Ando* 3312 (TENN). Mt. Mitsumine, *U. Mizushima* 8059 (TENN). Nippara, *U. Mizushima* 8110 (TENN). FUKUSHIMA PREF. Irimizu, *Y. Ikegami* 34030 (TENN). KUMAMOTO PREF. Koonose, *ca.* 100 m., *K. Mayebara* (*Musci Japonici* 126).

DISTRIBUTION: India, China (Yunnan) and Japan (Honshu, Shikoku and Kyushu).

2. **Homaliadelphus laevidentatus** (Okam.) comb. nov. *Homalia laevidentata* Okam., Jour. Coll. Sci. Imp. Univ. Tokyo, 36: 20. 1915. *Homaliadelphus targionianus* var. *laevidentatus* (Okam.) Nog., Jour. Hattori Bot. Lab. 4: 28. 1950. Dixon and Potier de

la Varde (1928) treated *Homalia laevidentata* as a synonym of *H. targionianus*, comparing the type collections of the two species. However, Noguchi (1950) raised it to varietal rank and distinguished it from *H. targionianus* by the smaller size, more obovate leaves, smaller capsules on short setae (1.5-3.0 mm.) and a more pilose calyptra. After an examination of the type of *H. laevidentatus*, I agree with Noguchi that it is different, but I believe it different enough to merit specific status. Its leaves are smaller and rounder than those of *H. targionianus* as shown on TABLE 2. The lengths of setae and urns of capsules of *H. targionianus* and *H. laevidentatus* are shown in TABLE 1.

TABLE 1. Statistical data on lengths of setae and urn of capsules of *H. targionianus* and *H. laevidentatus*.

Species and localities	Length of setae (average) mm.	Length of urns (average) mm.	Number of sporophytes examined
H. targionianus			
Griffith 2, India (on bark)	3.5-5.0(4.55)	1.8-2.0(1.90)	10
Griffith 444, India (on bark)	3.5-7.0(4.90)	1.2-2.2(1.86)	10
Holotype, India	5.0	...	1
Musci Selecti et Critici 24 Japan (on rock)	3.5-7.0(5.25)	1.8-2.0(1.90)	2
H. laevidentatus			
Holotype, Japan (on bark)	2.0-2.5(2.27)	1.2-1.5(1.40)	10

Although the species has been considered dioicous, no male plants have been described. In the type material of *H. laevidentatus*, I found many small male plants growing on leaves of female plants; and so the species is more accurately described as phyllodioicous. A detailed description of the male plants (*fig.* 12-19) follows:

Male plants small, growing on leaves of female plants. Protonema persistent, the filaments consisting of 1 row of rectangular cells, about 14 μ wide. Stems erect, 0.6-1.0 mm. high, much branched above, about 40 μ wide (0.25 mm. wide with leaves). Stem leaves slightly complanate-foliate in 4 rows, broadly ovate to rotundate from narrow base, asymmetric, entire, about 0.12 mm. long, 0.11 mm. wide at middle part of stem, distal basal portion slightly incurved or making a small lobe; leaf cells almost quadrate to hexagonal, about 10 × 10 μ, slightly larger toward the base. Perigonia terminal; outer perigonial leaves oblong-spatulate with sheathing base conspicuous at one side, about 0.34-0.4 mm. long,

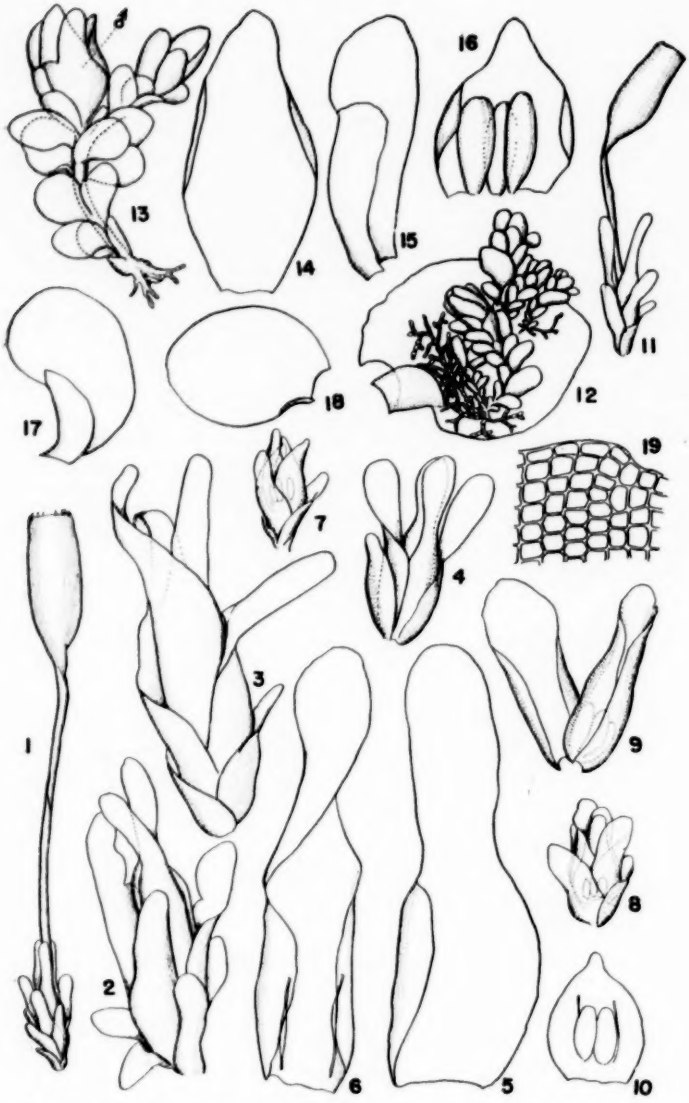

FIG. 1-10. *Homaliadelphus targionianus* (1, India, *Griffith* 444; 3, Japan, *Musci Selecti et Critici* 24; 2, 4-10, type). 1. Sporophyte, × 10. 2-4. Various stages of perichaetial buds, × 16.5. 5-6. Perichaetial leaves, × 43. 7-8. Perigonial buds, × 16.5. 9-10. Perigonial leaves, × 26.5. FIG. 11-19. *Homaliadelphus laevidentatus* (type). 11. Sporophyte, × 10. 12. Male plants on a leaf of a female plant, × 26.5. 13. A male plant, × 43. 14-16. Perigonial leaves, × 71.5. 17-18. Stem leaves, × 71.5. 19. Areolation at tip of stem leaf, × 308.

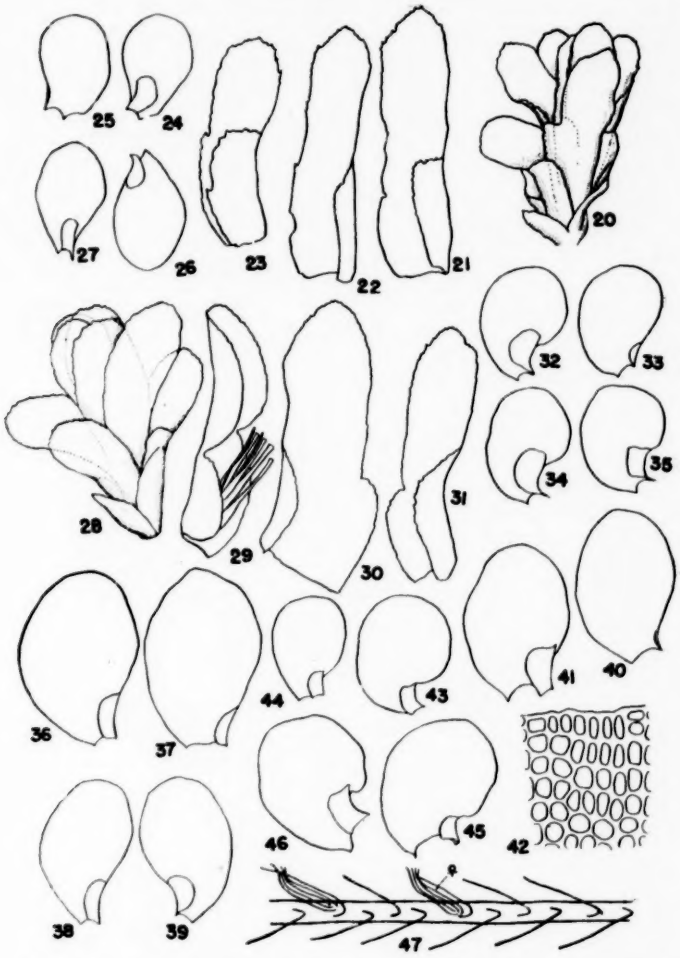

FIG. 20-27. *Homaliadelphus sharpii* (type). 20. Perichaetial bud, × 26.5. 21-23. Perichaetial leaves, × 43. 24-27. Stem leaves, × 16.5. FIG. 28-35. *Homaliadelphus sharpii* var. *rotundatus* (type). 28. Perichaetial bud, × 26.5. 29-31. Perichaetial leaves, × 43. 32-35. Stem leaves, × 16.5. FIG. 36-42. Stem leaves of *Homaliadelphus targionianus*. 36-39. From type, × 16.5. 40-42. From Japanese specimen (*Musci Selecti et Critici* 24), × 16.5. 42. Areolation at leaf tip, × 308. FIG. 43-46. Stem leaves of *Homaliadelphus laevidentatus* (type), × 16.5. FIG. 47. Diagram of leaf arrangement of *Homaliadelphus*.

inner leaves ovate with acute apices, about 0.45 mm. long, antheridia few, about 0.2 mm. long; paraphyses few.

SUBSTRATE: Tree bases.

SPECIMEN EXAMINED: Kiyomidudera, Prov. Idumo, Japan, *M. Nazaji*, March 13, 1913 (holotype, NICH).

DISTRIBUTION: Japan (Honshu and Shikoku); endemic; rare.

The phyllodioicous inflorescence indicates a significant difference from *H. targionianus* and, I think, justifies the recognition of an independent species. Small plants of *H. targionianus* were found infrequently on Indian materials (type specimen; *Griffith* 2 and 444). However, these proved to be young plants which were usually prostrate and longer than the male plants of *H. laevidentatus* and are not to be confused with them.

3a. HOMALIADELPHUS SHARPII (Williams) Sharp var. SHARPII, Castanea 9: 107. 1944. *Homalia sharpii* Williams, THE BRYOLOGIST 34: 20, *pl.* 2. 1931. The main characters distinguishing this species from *H. targionianus* are the irregularly serrate perichaetial leaves and smaller size. When we compare female buds (no sporophyte has been found on *H. sharpii*), the difference in size is remarkable. Those of *H. sharpii* are usually 0.5-1.5 mm. long, while those of *H. targionianus* are mostly 1.5-2.5 mm. long (except young buds; rarely perigonial buds of male plants might be confused with female buds) and are long-lingulate. Perichaetial leaves of *H. sharpii*, except the outer ones, are usually oblong or spatulate from a sheathing base, and the apex is apiculate to rounded with irregular serration. They are shorter, variously shaped, and have a less conspicuous sheath than those of *H. targionianus*.

Primary stems are prostrate, more densely and regularly branched than in *H. targionianus*. Secondary stems have leaves about 1-2 mm. wide. Leaves are smaller than those of *H. targionianus* (see TABLE 2). The usual size of the leaves of *H. sharpii* in the middle part of secondary stems is 0.77-1.06 × 0.59-0.83 mm., while those of *H. targionianus* are 1.34-1.58 × 0.99-1.08 mm. The species is apparently dioicous, but no male plants have been seen. Other characters are essentially the same as those of *H. targionianus*.

SUBSTRATE: Calcareous rocks.

SPECIMENS EXAMINED: U.S.A.: TENNESSEE; Near Agee, 1300 ft., *A. J. Sharp*, Mar. 20, 1930 (isotype, TENN). Along Coal Creek, 1100 ft., Anderson Co., *A. J. Sharp* (TENN). Savage's Garden, Coal Creek, Anderson Co., *A. J. Sharp* (*Musci Selecti et Critici* 71) (TENN), *Z. Iwatsuki* 425 (NICH). Cedar Creek, Campbell Co., *A. J. Sharp* (TENN). Near Marbledale, Knox Co., *A. J. Sharp* (TENN). VIRGINIA; Sinkhole near

Lucas Memorial Church, Giles Co., *P. M. Patterson & A. J. Sharp* V-190 (TENN.). MEXICO: South of Las Casas, Chiapas, *A. J. Sharp* 3411 (TENN).

DISTRIBUTION: Endemic to North America: western Virginia, eastern Tennessee and southern Mexico.

3b. **Homaliadelphus sharpii** var. **rotundatus** (Nog.) comb. nov. *Homaliadelphus targionianus* var. *rotundatus* Nog., Jour. Hattori Bot. Lab. 4: 28. 1950. This variety is similar in size and appearance to the American var. *sharpii*. The perichaetial leaves are very similar, except that those of var. *sharpii* are more strongly serrate to the base. However, var. *rotundatus* has more rounded stem leaves, about 1.1-1.3 times as long as wide, while those of var. *sharpii* are 1.3-1.5 times as long as wide (see TABLE 2). In var. *sharpii* the margins where lobes are attached are slightly curved to straight, while those of var. *rotundatus* are strongly curved. I believe this is a good variety, even though male plants and sporophytes are unknown.

SUBSTRATES: Calcareous rocks and bases of trees.

SPECIMENS EXAMINED: JAPAN: OITA PREF., Kawanobori-mura, *A. Noguchi* 14055, Sept. 10, 1939, holotype. Same locality, *A. Noguchi* (*Musci Japonici* 370) (TENN).

DISTRIBUTION: Japan (Honshu and Kyushu) and Formosa.

The known range of *H. sharpii* (*sensu lato*) now includes North America (Virginia, Tennessee and Mexico) and eastern Asia (Japan and Formosa). It clearly shows one of the typical disjunctive distributional patterns existing between eastern North America and eastern Asia which have been pointed out by Asa Gray and many other botanists. *Homaliadelphus* is usually restricted to lime-containing rocks in Japan and North America, but in India and Formosa it is more frequently found on the bases of trees. The finding of dwarf male plants on the leaves of female plants in the type of *H. laevidentatus* may suggest a tropical origin, since phyllodioicous inflorescences are more frequently found in mosses of tropical regions. Studies of the calcareous mosses of Japan indicate that there are many species of tropical or subtropical mosses on limestone in the southern portion of the country. If the genus *Homaliadelphus* originated from an old tropical (Oceanic) element, it is interesting to note that it is now restricted to a few, scattered temperate regions in Asia and North America as a relict genus.

No male plants of *Homaliadelphus sharpii* (*sensu lato*) have been found in Japan or eastern North America in spite of careful examination of the specimens. Dr. Sharp and I think that the sterility of the American plants may be due to the absence of male

plants. It can be recorded that the American variety reproduces by fragmentation and regeneration. This may also be true of Japanese plants.

TABLE 2. Statistical data on leaves of *Homaliadelphus targionianus, H. laevidentatus* and H. *sharpii*. (Two plants were selected from 10 collections, and 10 leaves were measured from the midportion of a secondary stem from each plant.)

Species and localities	Average length (μ)	Average width (μ)	Length-to-width ratio (L/W)
H. targionianus			
India, type	1513.0	969.4	1.560:1
	1245.1	837.0	1.487:1
India, *Griffith* 444	1127.3	768.4	1.467:1
	1375.3	908.9	1.513:1
Japan, *Musci Selecti et Critici* 24	1436.4	1086.8	1.328:1
	1341.4	995.6	1.356:1
Japan, *Musci Japonici* 126	1580.8	1033.6	1.538:1
	1417.4	1003.2	1.418:1
H. laevidentatus			
Japan, type	1079.2	843.6	1.297:1
	1003.2	752.4	1.342:1
H. sharpii var. *sharpii*			
Tennessee, type	777.0	591.4	1.314:1
	886.4	599.2	1.483:1
Virginia, *Patterson & Sharp* V-190	1064.0	786.6	1.358:1
	915.8	661.2	1.386:1
Mexico, *Sharp* 3411	1037.4	782.8	1.328:1
	976.0	699.2	1.397:1
H. sharpii var. *rotundatus*			
Japan, type	849.9	668.9	1.285:1
	786.8	649.0	1.192:1
Japan, *Musci Japonici* 370	988.0	809.4	1.230:1
	908.2	832.2	1.096:1

TABLE 2 lists the data collected from 10 collections (including four types) of the genus from Asia and North America. The length and width of 20 leaves on two different plants in each packet were measured, and the length-to-width proportions calculated. Two related species, *H. targionianus* and *H. laevidentatus*, have different leaf sizes: the leaves of *H. laevidentatus* are smaller and more obovate than those of *H. targionianus*. Of the two varieties of *H. sharpii*, var. *rotundatus* has more round leaves.

A scatter diagram (*fig.* 48) made from the same data shows more clearly the relationships between these four taxa. *Homalia-*

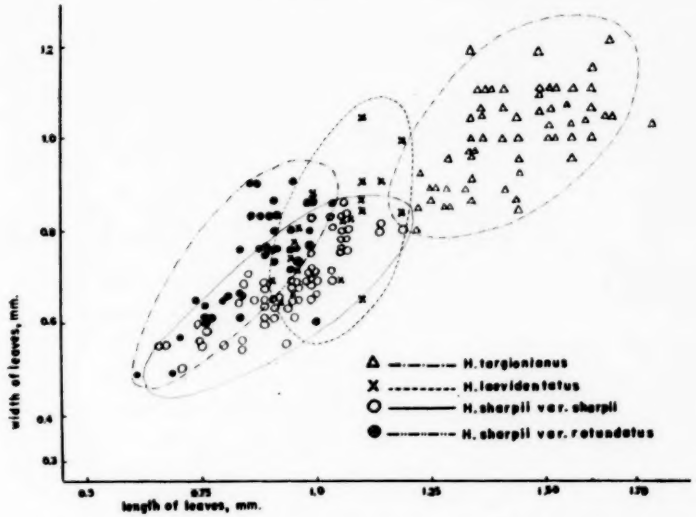

FIG. 48. Scatter diagrams showing the length and width of stem leaves of the species and varieties of *Homaliadelphus*.

delphus targionianus and *H. sharpii* are separated by leaf size. Of the two varieties of *H. sharpii*, the round leaves of var. *rotundatus* are indicated by a cluster of dots with a steeper axis. It is suggested that the two varieties are closely related to each other because of the overlap in clusters. However, not enough difference exists to separate them as species, since no distinction other than leaf shape has been recognized between these two taxa. The leaves of *H. laevidentatus* show a leaf size almost intermediate between *H. sharpii* and *H. targionianus*. They are variable but more like the leaves of *H. sharpii* in shape.

Wagner (1951) stated that the Mexican specimens of *H. sharpii* and also some recently collected in Tennessee approach the Asiatic plants (*H. targionianus*) more closely than does the type material. However, all collections of *H. sharpii* have different perichaetial leaves and smaller stem leaves than does *H. targionianus* as shown in TABLE 2. Gross comparisons between the four taxa are also shown in figure 48.

SUMMARY

All the taxa of the genus *Homaliadelphus*, which exhibits geographic disjunction between eastern North America and eastern Asia, were investigated taxonomically. The following new combinations were made: *Homa-*

liadelphus laevidentatus (Okam.) and *H. sharpii* var. *rotundatus* (Noguchi). The var. *laevidentatus* was raised to specific rank as a result of dwarf male plants being found on leaves of female plants and for other reasons, as well. It is suggested that the genus may be a relict of an old tropical element which now has a scattered distribution in temperate regions of eastern Asia and North America.

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NOTES ON CLADONIA, SUBGENUS CLATHRINA

WILLIAM MARTIN[1]

The subgenus Clathrina (Müll. Arg.) Wainio of the genus *Cladonia* comprises three species almost or wholly restricted to the Southern Hemisphere. It is characterized by much-branched, usually entangled podetia, with thick, smooth outer cortex of longitudinal hyphae, with as a rule copious and striking perforations, but lacking an inner chondroid layer, squamules, soredia and isidia.

In *Cladonia aggregata* the perforations are always less numerous than in either *C. retipora* or *C. sullivanii* and occasionally are almost lacking. Spermagonia and apothecia when present are small but numerous and usually dark brown or black in color. Of the

[1] 27 Merchiston St., Andersons Bay, Dunedin, New Zealand.

three species, *C. aggregata* alone ranges north of the equator, being found in the West Indies as well as in almost all land masses of the Southern Hemisphere. The other species are confined to Australasia. All three are common New Zealand indigens and in subalpine bogs commonly grow in association; but while *C. sullivanii* is almost restricted to bogs, the others have a wide range of habitats.

KEY TO THE CLATHRINAE

Sterile apices subulate. K±, P±.[2] ..... *C. aggregata*

Sterile apices obtuse. K—, P—.

Plants white or pale, coralloid, walls latticed and reticulate. Interior walls white. ..... *C. retipora*

Plants brown or blackish, perforations numerous. Interior walls seen through perforations black. ..... *C. sullivanii*

CLADONIA AGGREGATA (SW.) Ach. Primary thallus is unknown. As at present defined this species comprises a complex of diverse forms ranging in height from 3 or 4 mm. to well over 100 mm. tall and varying in color from pale stramineous to dark brown. Occasionally the plants may be greenish-brown or even ivory-white or cream-colored.

A dozen forms have received distinctive names; nine occur in New Zealand. Seen in their typical forms these are amply distinct; but intermediates are so abundant that none would appear to have defined limits and therefore to have real taxonomic status. In its numerous forms this species is one of the most abundant and widely distributed of the species indigenous to New Zealand.

The cylindrical form of the podetia and their branches is always in evidence though in some robust plants some flattening may occur. The perforations in the podetial walls may be fairly numerous, or they may be confined to restricted portions of the podetium, or they may sometimes be almost absent as in *F. imperforata.*

Typically the species is K— and P— but forms exist which are either K+ or P+. Thus two plants (no. 2153 and no. 2154) sent by me to Dr. A. W. Evans of Yale University were forwarded by him to Dr. Asahina, who expressed the opinion that they should probably be distinguished specifically from *C. aggregata* because they gave a good P+ reaction, indicating the presence of fumarprotocetraric acid. Even the normal barbatic acid may sometimes be lacking. It is clear that chemical distinctions are almost as numerous as morphological differences. Those botanists who recognize "chemical species" would doubtless split this "aggregate"

[2] K = aqueous solution of KOH. P = alcoholic solution of p-phenylenediamine.

species into a number of separate species or subspecies, but further study will be necessary to see how far chemical distinctions are accompanied by morphological differences. My only observation of this nature at present is that most specimens showing K+ reaction lack the normal brown color of the species.

Of the nine known to occur in New Zealand Allan (1937) stated that the commonest are forms *imperforata, pygmaea, racemosa* and *straminea;* to these I would add *cetrarioides.* However, in Allan's view as in my own, these are probably to be regarded as "in part habitatal, and in part due to varying degrees of sterility."

C. aggregata occurs most frequently in moist, partially shaded stations, but in bogs it is commonly fully exposed. Elsewhere it occurs in heaths, on rocks, on decaying logs or tussock stumps or on tree bases.

CLADONIA RETIPORA (LaBill.) Fr. Most authors have stated that the primary thallus does not exist or at least is unknown in any member of the Clathrina. In LaBillardier's original description of *Baeomyces retporus,* the primary thallus, according to Wainio (1887) is described as "crustaceus, granulis albissimis nitidis, conspersus, mox evanidus." For this reference I am indebted to Dr. Evans, who also corroborated my own discovery of plants from the Longwood Range in Southland with the primary thallus still present (no. 4480). He further observed that Duvigneaud, on the basis mainly of the absence of a primary thallus in all members of the Clathrina has proposed to raise the subgenus to generic rank under Nylander's original name Cladina and to place it on a new family termed the Clathrinaceae.

The undoubted existence of the primary thallus in my plants disposes at once of one main reason for the proposed new genus and family. However, the primary thallus has yet to be observed in the case either of *C. aggregata* or of *C. sullivanii* in which as in *C. retipora* the plants normally multiply vegetatively by development of new podetia from fragments of former podetia.

C. retipora is abundant in New Zealand especially in dry manuka heaths, on sterile soils and stony wastes, on mountain screes, in bogs and less frequently on fallen and decaying trees or on consolidated sand dunes. Whereas in Australia a brownish tinge is sometimes present, in New Zealand the plants are normally pure white, grey, grey-green, or faintly yellowish. Without doubt it is the most handsome and attractive member of the Cladoniaceae, closely resembling a mass of coral. The clumps vary in size up to 25 cm. in width.

CLADONIA SULLIVANII Müll. Arg. This species, though rather less common than either of the other two is far from rare, ranging as it does from the Volcanic Plateau in the center of North Island to the south of Stewart Island. Like the others it varies in size and robustness as well as in habit, but it usually retains its brown color intermingled frequently with black. One of its fairly constant features is the black color of the walls of the central canal. The perforations in the podetial walls as a result resemble black spots.

Dr. Asahina has shown that divaricatic acid is constantly present and for that reason may be regarded as diagnostic. Dr. Evans believes this to be the only *Cladonia* containing this lichen substance. Normally, there is no difficulty in recognizing this species at a glance, but sometimes there is considerable convergence towards *C. aggregata*. Thus my no. 2134, 2144 and 4440, which Evans at first diagnosed as *C. aggregata*, were found later by him to contain divaricatic acid which confirmed my own previous determination of no. 2134 as *C. sullivanii* on the basis of the blackish interior walls. It is in cases such as these that chemical tests are of great value.

C. sullivanii is a montane species almost restricted to bogs. In Southland, however, it is found at an altitude of only 200 meters at Kuriwao and in Stewart Island at altitudes of 100 meters and possibly less. The possibility of hybridization between *C. aggregata* and *C. sullivanii* requires investigation.

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STUDIES ON THE CHEMISTRY AND DISTRIBUTION OF NORTH AMERICAN LICHENS (10-13)

MASON E. HALE, JR.[1]

10. LOBARIA LINITA (Ach.) Rabh.

EXSICCATAE EXAMINED: Macoun, *Canad. Lich.* 74 (WELC), 75 (US).

[1] Smithsonian Institution, Washington 25, D. C. Herbarium specimens of each species from one or more of the following institutions were examined and annotated: Duke University, Farlow Herbarium, National Fungus Collections, Smithsonian Institution, Southern Illinois University, Universities of Michigan, Tennessee, Toronto, and Wisconsin, Wellesley College, West

CHEMISTRY. A colorless tridepside, tenuiorin, was present in all specimens, as proved by microchemical tests with G. A. o-T. (Asahina, 1949).

DISTRIBUTION. *Lobaria linita* (*Fig.* 1) is widespread in the coastal forests from Washington north to Alaska (*Fig.* 5). Large reddish apothecia occurred in 50% of the specimens.

11. LOBARIA OREGANA (Tuck.) Müll. Arg.

EXSICCATAE EXAMINED: Macoun, *Canad. Lich.* 118 (US), 160 (US), and 246 (FH, US); *Reliq. Tuck.* 90 (FH, isotype); Merrill, *Lich. Exs.* 33 (FH, WVA).

CHEMISTRY. Usnic and stictic acids were demonstrated in all specimens microchemically.

DISTRIBUTION. *Lobaria oregana* (*Fig.* 2) is a conspicuous corticolous lichen in the Pacific Northwest from Oregon to southern Alaska (*Fig.* 6), often collected with *L. linita*. It is easily differentiated from both *L. pulmonaria* and *L. linita* by the presence of yellow usnic acid. Apothecia were present in 52% of the specimens.

12. PARMELIA FINKII Zahlbr.

EXSICCATAE EXAMINED: Hale, *Lich. Amer. Exs.* 7 (US). Type from Williamsville, Wayne Co., Missouri, *Colton Russell* (MICH).

CHEMISTRY. Atranorine, entothein, and an unidentified colorless substance were identified in all specimens. Entothein gives the medulla a pale yellow color.

DISTRIBUTION. Until 1954, this distinctive isidiate lichen (*Fig.* 3) was known only on bark from the type locality in Missouri. In the last four years the writer has collected it very frequently on sandstone from northeast Texas and Kansas east to the Carolinas and Virginia in open oak woods (*Fig.* 7). It is absent on limestone and extremely rare on tree bark. Only three specimens besides the type have been seen in herbaria. The species has been overlooked or misidentified as juvenile *Parmelia saxatilis*, which it superficially resembles.

13. PARMELIA AURULENTA Tuck.

EXSICCATAE EXAMINED: Merrill, *Lich. Exs.* 1, 278 (FH, US, WVA, WELC); Hale, *Lich. Amer. Exs.* 61 (US); Macoun, *Canad. Lich.* 85(US, *sub. nom. Parmelia borencri* [*sic*] var. *rudecta*).

Virginia University, and Yale University. Field studies have been supported in the Ozark Mountains by Sigma Xi, in the Gulf Coastal States by the American Philosophical Society, and in the central Appalachian Mountains by the National Science Foundation.

FIG. 1. *Lobaria linita.* FIG. 2. *Lobaria oregana* (a portion of the holotype, Oregon, *E. Hall,* FH). FIG. 3. *Parmelia finkii* (on rock). FIG. 4a. *Parmelia aurulenta* (on rock); FIG. 4b. *Parmelia aurulenta* (on bark). *All photographs natural size.*

Fig. 5. Lobaria linita

Fig. 6. Lobaria oregana

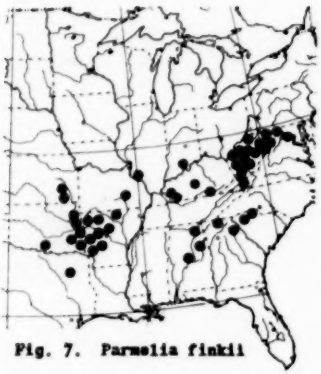

Fig. 7. Parmelia finkii

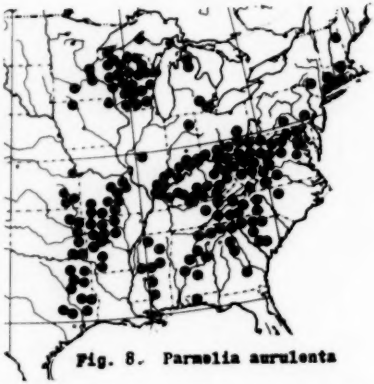

Fig. 8. Parmelia aurulenta

FIG. 5-8. Distribution of North American lichens. 5. *Lobaria linita* (24 localities). 6. *Lobaria oregana* (34). 7. *Parmelia finkii* (65). 8. *Parmelia aurulenta* (240).

CHEMISTRY. Atranorine and a yellow substance, probably entothein, in the medulla are constant components; zeroine may also be demonstrated in most specimens.

DISTRIBUTION. *Parmelia aurulenta* is one of the most common lichens in the eastern deciduous forest (*Fig.* 8), both on rocks (*Fig.* 4a) and on trees (*Fig.* 4b). In states which have been

more fully sampled (Arkansas, Wisconsin, Missouri, West Virginia) it is present in nearly 100% of the counties, frequently growing along with *Parmelia caperata, P. rudecta,* and *Pyxine sorediata.*

Degelius (1943) described a lichen from Togue Ponds, near Mount Katahdin, Maine, as *Parmelia silvestris* but later (1943a) reduced it to a variety of *P. aurulenta* after studying additional material from North Carolina and Tennessee. This lichen was distinguished from *P. aurulenta* by its well-delimited globose soralia as opposed to the diffuse soredial patches of the typical variety. The type specimen of *P. aurulenta* from the White Mountains of New Hampshire in Tuckerman's Herbarium (FH) and the isotype of *P. silvestris* in the United States National Museum are identical. Variation in the production of soredia is indeed very great, ranging from diffuse soralia (as in *Fig.* 4b) to the globose soralia described by Degelius and even to nearly isidiate coarse outgrowths (*Fig.* 4a) most common on plants from rock habitats.

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SOME LICHENS OF WESTERN ALASKA

GRACE E. HOWARD[1]

Our knowledge of Alaskan lichens is very limited. There are at present extensive areas in which very little if any collecting has been done. Most collections have been made in the coastal regions; however, the common use of long-range aircraft and bush pilots in "Piper Cubs" is helping to open up the interior. We urgently need more reports on the lichens of Alaska. Such reports will have to be the basis of any comprehensive flora of the region, and will eventually show the relation between Alaskan and eastern Siberian lichen floras. To further such information the writer has determined lichens from western Alaska sent to the University of Washington by various collectors and two collections sent by the

[1] University of Washington, Seattle, Wash. This work was made possible by a grant from the Biological and Medical Research Fund of the State of Washington.

United States National Museum for identification. Most Alaskan collections have been made as a second interest in some lonely situation or in time spent in awaiting transportation.

All of these specimens have been determined by the writer unless otherwise noted. They are in the Herbarium of the University of Washington unless indicated as follows: S—Naturhistoriska Riksmuseet, Stockholm; T—Private Herbarium of J. W. Thomson, Madison, Wisc.; US—U. S. National Herbarium, Washington, D. C.; WIS—Herbarium of the University of Wisconsin, Madison, Wisc.

The plants were collected by the following persons: ERNST ALMQUIST, leader of Expeditio Vegae, 1878-1880; V. H. CAHALANE, biologist in the National Park Service; ORAH DEE CLARK, teacher in government schools; OTTO WILLIAM GEIST, archaeologist; ROBERT M. HARDY, U.S. Armed Forces; GRACE A. HILL, teacher in government schools; JOHN KORANDA, plant ecologist; HAROLD J. LUTZ, professor of forestry; ERNEST H. MULLER, U. S. Geological Survey; MARIETTE PILGRIM, wife of an engineer at Stampede Mine; HENRY S. PRICE, U. S. Armed Forces; GEORGE W. RAWSON, biologist in veterinary science; JEANNETTE STEWART, arctic bibliographer; RUTH D. SVIHLA, bryologist; RHODA THOMAS, teacher in government schools, and her husband, W. E. THOMAS; DAN Q. THOMPSON, lemming ecologist; PAUL TINKER, student. These collectors will be referred to only by surnames, except for W. E. Thomas.

APPROXIMATE LATITUDES AND LONGITUDES OF LOCALITIES

AKOKPAK, 59° 36′ N, 157° 6′ W. AKUTAN ISLAND, 54° 9′ N, 165° 47′ W, one of the eastern Aleutians. AMERICAN RIVER near Hammersley's Cabin, 59° 2′ N, 155° 38′ W. ANIAK, on Yukon Watershed, about 40 mi. NW. of Aniak, 62° 5′ N, 160° 10′ W. ATTU ISLAND, 52° 53′ N, 173° E, the most westerly of the Aleutian chain. FOX, 64° 57′ N, 147° 41′ W, on the Elliot Highway, about 8 mi. N. of Fairbanks. GOODNEWS BAY, 59° 2′ N, 161° 40′ W, on Bering Sea. HAGEMEISTER ISLAND, 58° 38′ N, 161° 8′ W, in Bering Sea. ILIAMNA MORAINE, 59° 31′ N, 156° 13′ W. KASIGLUK, 60° 50′ N, 162° 40′ W, vicinity of Bethel. KATMAI NATIONAL MONUMENT, south of Grosvenor Lake, on portage to Bay of Islands, 58° 41′ N, 155° 25′ W. KIANA, 66° 58′ N, 160° 27′ W. KING SALMON (Naknek Air Field), 58° 40′ N, 156° 36′ W. KVICHAK MORAINE, 59° 31′ N, 156° 13′ W. MCCALLUM, 63° 14′ N, 145° 36′ W, on Richardson Highway. MENTASTA VILLAGE, 62° 55′ N, 143° 51′ W, on Glenn Highway. NANWHYENUK LAKE, 4 mi. NNE. of outlet, 59° 2′ N, 155° 38′ W, on Alaska Peninsula. PERRYVILLE, 55° 55′ N, 159° 10′ W, on Alaska Peninsula. "PIKE KNOB," 58° 43′ N, 159° 27′ W, on Nushagak Peninsula. POINT BARROW, 71° 23′ N, 156° 30′ W. PORT CLARENCE, 65° 15′ N, 166° 30′ W, on Bering Strait. PORT HEIDEN, 56° 58′ N, 158° 38′ W, on Alaska Peninsula. Seward, 60° 6′ N, 149° 26′ W, along the Anchorage-Seward Road, about 15 mi. N. of Seward. SINUK, 64° 36′ N, 166° 15′ W, near Nome. STAMPEDE, 63° 41′ N, 150° 25′ W, on NW. boundary of Mt. McKinley National Park. ST. LAWRENCE ISLAND, in Bering Sea: *Boxer Bay*, 63° 21′ N, 171° 35′ W; [*unnamed locality*, collections of Expeditio Vegae], 63° 50′ N, 171° 30′ W; *Savoogna*, 63° 42′ N, 170° 25′ W. STUYAHOK CAMP LAKE, WNW. of lake, 59° 51′ N, 156° 30′ W. TAKOTNA, 63° N, 156° 4′ W. TANANA, 65° 11′ N, 152° 6′ W. THOMPSON PASS, 61° 7′ N, 145° 53′ W, 20 mi. NW. of Valdez. UMIAT, 69° 23′ N, 152° 10′ W. UNALASKA ISLAND, 53° 52′ N, 166° 45′ W, one of the larger Aleutians.

UTUKOK RIVER (mouth of), 70° 15′ N, 162° 15′ W. VOLCANO VENIAMIN, 56° 4′ N, 159° 10′ W, on Alaska Peninsula.

LIST OF SPECIES*

ALECTORIA JUBATA (L.) Ach. Nanwhyenuk Lake, on *Picea glauca*, Aug. 2, 1951, *Muller* 855, common. Stampede, on dead spruce branches, about 1500 ft., June 18, 1953, *Pilgrim* 132.

ALECTORIA NIGRICANS (Ach.) Nyl. Port Heiden, on ground, Sept. 1942, *Price* 1. "Pike Knob," in tundra, June 25, 1951, *Muller* 672. Kasigluk, near dry lake, in wet tundra, Sept. 19, 1954, *Thomas* L-4.

ALECTORIA OCHROLEUCA (Ehrh.) Nyl. Port Heiden, on ground, Sept. 1942, *Price* 7. Attu Island, Siddens Valley, Engineers Canyon, on rocky ledges, April 11, 1945, *Hardy* 14. Stampede, on lava rocks, about 5000 ft., *Pilgrim* 252. Kasigluk, near dry lake, in wet tundra, Sept. 19, 1954, *Thomas* L-4a; near school, in damp tundra, Sept. 17, 1955, *Thomas* L-2, L-3, L-7, L-8; in tundra, May 29, 1956, *Tinker*. Abundant in certain regions and eaten by the older Eskimos when cooked with fish or other meat.

CALOPLACA ELEGANS (Link.) Th. Fr. Stampede, on rocks, about 5000 ft., July 5, 1953, *Pilgrim* 249.

CETRARIA CUCULLATA (Bell.) Ach. Tanana, Sept. 1911, *Clark* 10. Port Heiden, on ground, Sept. 1942, *Price* 3. Stuyahok Camp Lake, Aug. 15, 1951, *Muller* 932. Umiat, along the Colville River in tundra, July 16, 1952, *Rawson* (US). Kasigluk, near school, in damp tundra, Sept. 17, 1955, *Thomas* L-9, L-14. A common and widely distributed Alaskan Lichen.

CETRARIA CLAUCA (L.) Ach. Tanana, Sept. 1911, *Clark* 14.

CETRARIA ISLANDICA (L.) Ach. Tanana, Sept. 1911, *Clark* 11. Port Heiden, in tundra, Sept. 1942, *Price* 4. Volcano Veniamin, near the volcano, on ground, June 10, 1946, *Stewart*. Kasigluk, near dry lake, in wet tundra, Sept. 19, 1954, *Thomas* L-12, and Sept. 17, 1955, *Thomas* L-12. A common lichen in Alaska. One of the chief foods of reindeer, also a very important human food in some northern countries. Var. *SUBTUBULOSA Fries. Attu Island, Siddens Valley, on heather slopes and moss-covered ledges, April 11, 1945, *Hardy* 10a, 10b.

CETRARIA LACUNOSA var. MACOUNII DR. Port Heiden, on dead twigs, Sept. 1942, *Price* 2. Attu Island, Siddens Valley, Engineers Canyon, on rather dry rock ledge, April 21, 1945, *Hardy* 30. Not previously known from the mainland of Alaska, but reported from Adak, Atka and Unalaska Islands (Degelius, 1937).

CETRARIA NIVALIS (L.) Ach. Port Heiden, on ground, Sept. 1942, *Price* 6. "Pike Knob," in tundra, June 23, 1951, *Muller* 671. Kvichak Moraine, July 18, 1951, *Muller* 792. Stampede, on wet shaded slope, about 2000 ft., June 14, 1953, *Pilgrim* 244.

CETRARIA PINASTRI (Scop.) Röhl. Port Heiden, on bark, Sept. 1942, *Price* 5. Stampede, on dead wood, June 15, 1953, *Pilgrim* 134. Not often collected in Alaska.

CETRARIA RICHARDSONII Hook. Stampede, on alpine slopes, about 4000 ft., July 12, 1953, *Pilgrim* 251. A rare Alaskan lichen, previously reported only from Eagle (Herre, 1920) and near Mt. McKinley National Park Railroad Station (Hanson, 1951).

CETRARIA TENUIFOLIA (Retz.) R. H. Howe, Jr. Kasigluk, near dry lake,

* So far as I have been able to ascertain the 5 species or varieties marked with an asterisk have not been reported previously from Alaska.

in wet tundra, Sept. 19, 1954, *Thomas* L-4a. Previously reported only from Unalaska, Atka, Attu and St. Paul Islands (Degelius, 1937).

CETRARIA TILESII Ach. Port Heiden, on decaying tundra plants, Sept. 1942, *Price* 8. Stampede, on wet shaded slope, about 2000 ft., June 14, 1953, *Pilgrim* 244a. Previously reported only from Kotzebue (Hanson, 1951).

CLADONIA ALPESTRIS (L.) Rabh. Port Heiden, on thin layer of soil over rocks, June 1943, *Price* 9 (det. Evans). Attu Island, Siddens Valley, East Canyon, on grass slope, about 175 ft., April 1, 1945, *Hardy* 4. Fo. ABERRANS des Abb. Takotna, Nov. 7, 1934, *Clark*. Port Heiden, on soil in rock crevices, June 1943, *Price* 10. St. Lawrence Island, Savoogna, on bluff above the sea, on large volcanic boulder, June 7, 1946, *Stewart* (det. Evans). Stampede, on boggy slope, about 2000 ft., June 21, 1953, *Pilgrim* 247. Fox, in muskeg, Aug. 13, 1954, *Svihla*. Kasigluk, near school, in damp tundra, Sept. 17, 1955, *Thomas* L-13. Widely distributed in Alaska.

CLADONIA AMAUROCRAEA fo. CELOTEA (Ach.) Wainio. Attu Island, Siddens Valley, Engineers Canyon, on rock ledges, April 11, 1945, *Hardy* 9 (det. Evans). Stuyahok Camp Lake, Aug. 15, 1951, *Muller* 932a. Akokpak, in spruce-birch parkland, Aug. 23, 1951, *Muller* 951. Stampede, in wet mossy area, about 1500 ft., on marshy slope, about 2000 ft., June 20, 1953, *Pilgrim* 140, 245d (both det. Evans). Common in Alaska. Fo. OXYCERAS (Ach.) Wainio. Fox, in muskeg, Aug. 13, 1954, *Svihla*. Kasigluk, near the school, in damp tundra, Sept. 17, 1955, *Thomas* L-6.

CLADONIA BELLIDIFLORA (Ach.) Schaer. Tanana, Sept. 1911, *Clark* 6. Attu Island, Siddens Valley, Engineers Canyon, on mossy rocks and heather slopes, April 11, 1945, *Hardy* 12a, 13. A common and widely distributed Alaskan lichen.

CLADONIA CENOTEA (Ach.) Schaer. Fox, in muskeg, Aug. 13, 1954, *Svihla* (det. Thomson).

CLADONIA CHLOROPHAEA (Flk.) Spreng. Attu Island, Siddens Valley, on mossy rocks and on ground at margins of snow slides, April 11, 1945, *Hardy* 13b (det. Evans). Stampede, in boggy area on decaying wood and moss, about 2000 ft., June 18, 1953, *Pilgrim* 248b. Kasigluk, near the school in wet tundra, Sept. 17, 1957, *Thomas* L-15.

CLADONIA COCCIFERA (L.) Willd. Sinuk, 1915, Hill. Port Heiden, in tundra, June 1943, *Price* 12. Attu Island, Siddens Valley, on mossy rocks and on ground at the margins of snow slides, April 11, 1945, *Hardy* 13a (det. Evans). Stampede, on dry ridge, about 3500 ft., May 31, 1953, *Pilgrim* 30. Thompson Pass, in muskeg, Aug. 16, 1954, *Svihla*. A common lichen in Alaska.

CLADONIA CORNUTORADIATA (Coem.) Sandst. Stampede, in boggy area, about 2000 ft., June 18, 1953, *Pilgrim* 248c. Kasigluk, near the school in wet tundra, Sept. 17, 1955, *Thomas* L-15 (det. Evans). Previously reported only from Cape Nome and Kotzebue (Merrill, 1929).

CLADONIA DEFORMIS (L.) Hoffm. Tanana, Sept. 1911, *Clark* 7, 8. Stampede, in boggy area, 2000 ft., June 18, 1953, *Pilgrim* 248. Kasigluk, near dry lake in wet tundra, Sept. 19, 1954, *Thomas* L-2 Fo. *CRENULATA Ach. Fox, in muskeg, Aug. 13, 1954, *Svihla* (det. Thomson).

CLADONIA GRACILIS var. CHORDALIS (Flk.) Schaer. Attu Island, Siddens Valley, Engineers Canyon, on mossy rocks and heather slopes, April 11, 1945, *Hardy* 12b. A common lichen on the Aleutians. Fo. *DILACERATA Flk. Stampede, in boggy area, about 2000 ft., June 18, 1953, *Pilgrim* 248a. Var. ELONGATA (Jacq.) Flk. Attu Island, Siddens Valley, Engineers Canyon,

on mossy and heather slopes, April 11, 1945, *Hardy* 11. Stampede, about 2000 ft., May 27, 1953, *Pilgrim* 16. Often reported from Alaska.

CLADONIA MITIS Sandst. Attu Island, Siddens Valley, Engineers Canyon, on rock ledges, April 11, 1945, *Hardy* 9a.

CLADONIA PYXIDATA var. POCILLUM (Ach.) Flot. Thompson Pass, in muskeg, Aug. 16, 1954, *Svihla*.

CLADONIA PLEUROTA (Flk.) Schaer. Tanana, Sept. 1911, *Clark* 2.

CLADONIA RANGIFERINA (L.) Web. Volcano Veniamin, near the volcano on ground, June 10, 1946, *Stewart*. Stampede, on marshy slope, about 2000 ft., June 20, 1953, *Pilgrim* 245c. Fox, in muskeg, Aug. 13, 1954, *Svihla*. A very abundant and widely distributed *Cladonia*.

CLADONIA SQUAMOSA (Scop.) Hoffm. Stampede, near edge of peat bog, about 2000 ft., July 8, 1953, *Pilgrim* 256.

CLADONIA SYLVATICA (L.) Hoffm. Port Heiden, in tundra, June 1943, *Price* 8b (det. Evans). Stampede, on marshy slope, about 2000 ft., June 20, 1953, *Pilgrim* 245a. Common Alaskan lichen.

CLADONIA UNCIALIS (L.) Web. Kiana, on hillside in tundra, Aug. 1937, *Clark*. Perryville, in front of village, on boulder near high tide mark, June 10, 1946, *Stewart* (det. Evans). Akutan Island, Akutan Village, on dry rocks among shrubs, June 13, 1946, *Stewart* (det. Evans). In a letter Dr. Evans wrote, "This is the first *Cladonia* I have seen from Akutan Island."

CORNICULARIA DIVERGENS Ach. Port Heiden, Sept. 1942, Price 1a. Hagemeister Island, Aug. 21, 1953, *Muller* 1324. First report from this island. Kasigluk, in tundra, May 29, 1956, *Tinker*, who says, "abundant in this area, often eaten by the older Eskimos when cooked with fish or other meat." Widely distributed in Alaska. Fo. GRACILIS DEGEL. "Pike Knob," in tundra, June 25, 1951, *Muller* 672a. The only previous Alaskan records are Unalaska and Semichi Islands (Degelius, 1937).

DACTYLINA ARCTICA (Hook.) Nyl. Umiat, Colville River bottom, Aug. 9, 1952, *Rawson* (US). Stampede, on an alpine slope, about 4500 ft., July 11, 1953, *Pilgrim* 246. A typically northern lichen.

*EVERNIA PRUNASTRI (L.) Ach. Stampede, on dead spruce branches, about 1500 ft., June 15, 1953, *Pilgrim* 133.

HAEMATOMMA VENOSUM (L.) Mass. Port Heiden, on rock, July, 1943, *Price* 13. Attu Island, Dam Creek, on rock cliff, about 200 ft., May 27, 1945, *Hardy* 72.

ICMADOPHILA ERICETORUM (L.) Zahlbr. Fox, growing in *Sphagnum*, Aug. 13, 1954. *Svihla*. Rather a rare lichen in Alaska.

LEPTOGIUM LICHENOIDES var. PULVINATUM (Hoffm.) Zahlbr. Port Heiden, in damp tundra, July, 1943, *Price* 17. Previously reported only from southeastern Alaska (Magnusson, 1932).

LOBARIA LINITA (Ach.) Rabh. Attu Island, Siddens Valley, on mossy rocks, April 19, 1945, *Hardy* 21.

LOBARIA PULMONARIA (L.) Hoffm. American River, Aug. 3, 1951, *Muller* 854. Not common in Alaska.

NEPHROMA ARCTICUM (L.) Torss. Simuk, 1915, *Hill*. Attu Island, near Lake Nicholas, on grass heather slope, 50 ft., June 2, 1945, *Hardy* 86. King Salmon, about 2.5 miles NNE. of Airways Communications Station, Aug. 5, 1951, *Muller* 856, common. Akokpak, in spruce-birch parkland, on ground, Aug. 23, 1951, *Muller* 953. Hagemeister Island, Aug. 21, 1953, *Muller* 1346. First report from this island. A common Alaskan lichen.

NEPHROMOPSIS CILIARIS (Ach.) Hue. Kasigluk, near the school in damp

tundra, Sept. 17, 1955, *Thomas* L-1. Not common so far north, but reported from Kodiak I. (Cummings, 1904) and Adak I. (Stair, 1948).

Ochrolechia frigida (Sw.) Lynge. Mentasta Village, from a white spruce stand on a gravelly plain, growing over moss, Aug. 25, 1950, *Lutz* 50-256 (WIS; det Thomson). Point Barrow, Central Marsh on abandoned beach, Aug. 28, 1951, *Thompson* (WIS; det. Thomson). Iliamna Moraine, 3 mi. west of camp, in tundra mat on moraine, July 18, 1951, *Muller* 788. Point Barrow, on moss, July 5, 1953, *Koranda* AL-9 (WIS). Fo. gonatodes (Ach.) Lynge. St. Lawrence Island, Expeditio Vegae 1878-1880, July 1879, *Almquist* (S). Unalaska Island, Univ. of Calif. Exped. to Alaska, June-July 1899 (US). Goodnews Bay, near Platinum, growing over moss, 1933, *Geist* (T). St. Lawrence Island, Boxer Bay, on ground, 1933, *Geist* (T) Port Heiden, on soil, July 1943, *Price* 15. Fo. thelephoroides (Th. Fr.) Lynge. St. Lawrence Island, Expeditio Vegae 1878-1880, July 1879, *Almquist* (S). St. Lawrence Island, Savoonga, on the ground, 1933, *Geist*. Point Barrow, Central Marsh, on abandoned beach, Aug. 28, 1951, *Thompson* (WIS; det. Thomson). Point Barrow, one mile south of Barrow Base, on beach ridge, on moss, July 11, 1953, *Koranda* AL-18b (WIS; det. Thomson).

Ochrolechia inaequatula (Nyl.) Zahlbr. Port Clarence, Expeditio Vegae, 1878-1880, July, 1879, *Almquist* (S).

Ochrolechia tartarea (L.) Mass. St. Lawrence Island, Expeditio Vegae, 1878-1180, July, *Almquist* (S).

Ochrolechia upsaliensis (L.) Mass. Port Clarence, Expeditio Vegae, 1878-1880, July 1879, *Almquist* (S).

Parmelia centrifuga (L.) Ach. Port Heiden, in thin layer of soil over rock, Aug. 1943, *Price* 16. Katmai National Monument, on a boulder, July 17, 1954, *Cahalane*. Only previous collections: Seward Peninsula (Herre, 1920) and Camden Bay (Merrill, 1924).

Parmelia enteromorpha Ach. Port Heiden, on bark, July 1943, *Price* 20. Not common so far north as Alaska.

Parmelia olivacea (L.) Ach. Port Heiden, on bark, July 1943, *Price* 18. An inconspicuous lichen; this perhaps accounts for the few reported collections.

Parmelia omphalodes (L.) Ach. Attu Island, Siddens Valley, Engineers Canyon, on rock cliff, about 200 ft., April 29, 1945, *Hardy* 58. A common northern lichen; a number of collections have been reported from the Aleutians.

Parmelia physodes (L.) Ach. Stampede, on dead spruce, about 1400 ft., July 20, 1953, *Pilgrim* 253.

Parmelia pubescens (L.) Wainio. Port Heiden, in tundra, Aug. 1943, *Price* 24.

Parmelia saxatilis (L.) Ach. Port Heiden, on rocks, Aug. 1943, *Price* 19. Hagemeister Island, Aug. 21, 1953, *Muller* 1355. First report from this island. A common and widely distributed lichen in Alaska.

Parmelia sulcata Tayl. Port Heiden, on soil in tundra and on decaying wood, Aug. 1943, *Price* 21, 23. Often reported from Alaska.

Peltigera aphthosa (L.) Willd. var. aphthosa. Port Heiden, Sept. 1943, *Price* 22. Attu Island, Siddens Valley, on thick layers of moss over rock, April 19, 1945, *Hardy* 24, 27. Utukok River, in open spaces among willows, on driftwood, Aug. 3, 1952, *Ratcson* (US). Stampede, in a marshy area, about 1500 ft., May 24, 1953, *Pilgrim* 13. Seward, in muskeg, Aug. 16, 1954, *Svihla*. Reported many times from Alaska (Thomson, 1950). Very common and widely distributed. Var. variolosa (Mass.) Thomson. Attu

Island, Siddens Valley, on rocks along creek. April 23, 1945; Holtz-Sarana Pass, on base of a boulder in a shady spot, July 16, 1945, *Hardy* 41, 221. Stampede, in moist shady area, about 2100 ft., June 28, 1953, *Pilgrim* 254. Aniak, Sept. 17, 1955, *W. E. Thomas* L-17a. Not so common in Alaska as var. *aphthosa*.

PELTIGERA CANINA (L.) Willd. Attu Island, Siddens Valley, on mossy rocks, April 19, 1945, *Hardy* 22. Common in Alaska, as over all North America (Thomson, 1950). Var. ALBESCENS (Wahlbr.) Thomson. Aniak, Sept. 17, 1955, *W. E. Thomas* L-17.

PELTIGERA MALACEA (Ach.) Funck. King Salmon, Civil Aeronautics Administration, in dry heath vegetation, July 1, 1953, *Muller* 1123 (det. Thomson). A rare lichen in Alaska.

PELTIGERA POLYDACTYLA var. CRASSOIDES Gyel. Attu Island, Siddens Valley, on mossy rocks, April 19, 1945, *Hardy* 23 (det. Thomson). Stampede, on a marshy slope, about 2000 ft., June 20, 1953, *Pilgrim* 245b. A rare *Peltigera*.

PHYSCIA MUSCIGENA (Ach.) Nyl. Port Heiden, on soil among mosses, Sept. 1943, *Price* 25.

RAMALINA ALMQUISTII Wainio. Port Heiden, on thin layer of soil over rock, Sept. 1942, *Price* 27. Attu Island, Dam Creek, on rock cliff, about 200 ft., May 27, 1945, *Hardy* 69 (ver. Magnusson). The first report from Attu Island. Only previous records are St. Paul I. (Du Rietz, 1925) and Unalaska, Atka, Adak and Agattu Islands (Degelius, 1937).

SIPHULA CERATITES (Wahlbr.) Fries. Attu Island, Siddens Valley, margins of small streams and snow patches, about 125 ft., May 26, 1945, *Hardy* 75. Kvichak Moraine, first plant to enter invading gravels of drying lake, July 18, 1951, *Muller* 790. Previously reported from Attu Island, Icy Cape, Seward Peninsula (Ardwisson, 1926) and Thum Bay (Eyerdam, 1949).

SOLORINA CROCEA (L.) Ach. Attu Island, Siddens Valley, Engineers Canyon, on rather dry rock cliff, May 10, 1945, *Hardy* 64. Common on the Aleutians.

SPHAEROPHORUS GLOBOSUS (Huds.) Wainio. Tanana, Sept. 1911, *Clark* 12. Akokpak, in a spruce-birch parkland, Aug. 23, 1951, *Muller* 952. Common and widely distributed.

STEREOCAULON ALPINUM Laur. Unalaska Island, Dutch Harbor, growing among moss on ground, June 18, 1946, *Stewart*. Stampede, in boggy area, about 1500 ft., June 20, 1953, *Pilgrim* 130. Hagemeister Island, Aug. 21, 1953, *Muller* 1337; first record from this island McCallum, on soil, Aug. 1954, *Szihla* (det. Lamb).

STEREOCAULON INTERMEDIUM (Sav.) H. Magn. Attu Island, Siddens Valley, Engineers Canyon, about 200 ft., on rock ledges, April 26, 1945, *Hardy* 56a (det. Lamb).

STEREOCAULON PASCHALE (L.) Hoffm. Stampede, marshy slope, about 2000 ft., June 20, 1953, *Pilgrim* 245 (det. Lamb).

STEREOCAULON TOMENTOSUM Fries. Port Heiden, on soil, Sept. 1943, *Price* 28 (det. Lamb).

THAMNOLIA VERMICULARIS (Sw.) Schaer. Port Heiden, in dry tundra with moss and other lichens, Sept. 1943, *Price* 26. Volcano Veniamin, near the volcano, on ground, June 10, 1946, *Stewart*. Kvichak Moraine, on moraine mat, July 18, 1951, *Muller* 781. Stampede, on wet shaded slopes, about 2000 ft., June 14, 1953, *Pilgrim* 244b. Kasigluk, near dry lake, in wet tundra, Sept. 19, 1954; Sept. 17, 1955, *Thomas* L-5, L-10. A widespread arctic lichen.

UMBILICARIA HYPERBOREA (Ach.) Hoffm. Port Heiden, on rocks, Sept. 1943, *Price 29*. Stampede, on lava rocks, about 5000 ft., July 5, 1953, *Pilgrim 252a*. Many records from Alaska (Llano, 1950).

UMBILICARIA PROBOSCIDEA (L.) Schrad. Port Heiden, on rock, June 1943, *Price* 14. Attu Island, Siddens Valley, Engineers Canyon, on rock cliff about 200 ft., May 11, 1945, *Hardy* 65. Hagemeister Island, Aug. 21, 1953, *Muller* 1322. First report from this island. Many records from Alaska (Llano, 1950).

*USNEA GLABRATA (Ach.) Wainio. Stampede, on dead branches of spruce, June 15, 1953, *Pilgrim* 131 (det. Herre).

XANTHORIA CANDELARIA (L.) Kickx. Port Heiden, on twigs, Sept. 1943, *Price* 30. Attu Island, Dam Creek, on rock cliff, about 200 ft., *Hardy* 71.

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——— & JEAN PEARCE. The occurrence and functions of the stomata in British bryophytes. II. Functions and physiology. *Ibid.* 3(2): 242-259. 1957. [List of 160 genera with approximate no. of stomata observed in each]

POTIER DE LA VARDE, R. Contribution à la flore bryologique afraicaine (9e article). Rev. Bryol. et Lichén. 26 (1/2): 1-7. 4 *fig.* 1957. [New: *Gymnostomiella* (?) *rosulata* n. sp., *Campylopus mozambicus* n. sp. (in subg. Eucampylopus, sect. Atrichi), *Leucoloma Schelpei* n. sp. (sect. Euvittata), *Daltonia constricta* n. sp., *Calyptothecium Woodii* n. sp. (sect. Pseudoneckera), *Microthamnium brevicuspes* (P. de la V.) n. c.]

REDFEARN, P. L. JR. Rediscovery of *Solmsiella kurzii*. THE BRYOLOGIST 60(4): 337-338. 1957. [In Jefferson Co., Florida]

REESE, W. D. A new species and a new combination of *Calymperes*. THE BRYOLOGIST 60(4): 335-337. 1957. [New: *C. meyeri* n. sp., *C. venezuelanum* (Mitt.) n. c.]

SANNOMIYA, M. Chromosome studies of mosses. II. Jour. Hattori Bot. Lab. 18: 98-101. 23 *fig.* 1957.

SHERRARD, ELIZABETH M. Bryophytes of Alaska. II. Additions to the mosses and hepatics of the Mt. McKinley Region. THE BRYOLOGIST 60(4): 310-326. 1957. [136 mosses, 25 hepatics; new: *Hypnum lindbergii* v. *elatum* (Schimp.) n. c.]

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SVIHLA, RUTH D. Frullaniaceae of Burma. II. *Frullania shanensis* n. sp. THE BRYOLOGIST 60(4): 359-363. 20 *fig.* 1957.

SZWEYKOWSKI, J. Materialy do geografii watrobówcow polskich. I. Rozmieszczenie watrobówca *Barbilophozia Kunzeana* (Hüb.) K. M. w Polsce. Acta Soc. Bot. Poloniae 25(4): 589-602. 3 *maps.* 1956.

———. Materialy do geografii watrobówcow polskich. II. *Chandonanthus setiformis* (Ehrh.) Howe w Tatrach Polskich. *Ibid.* 25(4): 603-613. 1 *fig.* 1 *map.* 1956.

TAKAKI, N. Certain mosses are utilized by birds and insects. Misc. Bryol. et Lichén. 12: 1-2. *Fig.* 1957. [Japanese]

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TATEBE, E. The utilization of some mosses. Misc. Bryol. et Lichén. 11: 3. 1957. [Japanese]

VAN DER WIJK, R. Precursory studies in Malaysian mosses. I. Revision of the genus *Dawsonia* R. Brown. Rev. Bryol. et Lichén. 26(1/2): 8-19.

5 *fig.* 1957. [14 taxa; key; new: *D. pulchra* n. sp., *D. celebensis* n. sp., *D. lativaginata* n. sp.]

WALLACE, E. C. *Tortella inflexa* (Bruch) Broth. in Britain. [Bryological Notes] Trans. British Bryol. Soc. 3(2): 308. 1957.

WARBURG, E. F. Two mosses from Scotland, new to the British Isles. Trans. British Bryol. Soc. 3(2): 171-173. 1957.

WATANABE, R. Geographical range of *Tetrodontium brownianum* in Mt. Azuma. Misc. Bryol. et Lichen. 9: 3. 1957. [Japanese]

WEBER, W. A. *Tortula papillosa* in New Mexico. THE BRYOLOGIST 60(2): 143-145. 1957.

WEILL, J. *Buxbaumia aphylla* L. dans la forêt de Fontainebleau. Rev. Bryol. et Lichén. 26(1/2): 86. 1957.

WELCH, WINONA. Mosses of Indiana: an illustrated manual. 478 *pp.* 254 *fig.* 1 *map.* Indiana Dept. Conservation, Div. Forestry. The Bookwalter Co., Indianapolis. 1957. [217 spp., 34 var., 9 forms, in 25 families]

WYLIE, ANN. The chromosome numbers of mosses. Trans. British Bryol. Soc. 3(2): 260-278. 1 *tab.* 1957. [364 species in the table]

RECENT LITERATURE ON LICHENS—25[1]

WILLIAM L. CULBERSON[2]

ALLARD, H. A. Occurrence of the lichen *Cetraria islandica* Ach. in Virginia and West Virginia. Castanea 22(2): 106-109. 1957.

[ANDREEV, V. N.][3] [Growth of forage lichens and methods of improving it.] Geobotanica [Akad. Nauk SSSR, Bot. Inst. Trudy ser. 3] 9: 11-74. 14 *fig.* 28 *tab.* 1954.

[ASAHINA, Y.][4] [The manners in asking the name of lichens.] Misc. Bryol. et Lichen. [Japan] 10: 1. 1957.

BESCHEL, R. E. A project to use lichens as indicators of climate and time. Arctic 10(1): 60. 1957.

BOULY DE LESDAIN, M. Notes lichénologiques. N° XLII. Bull. Soc. Bot. France 104(5-6): 320-321. 1957. [8 spp. New: *Anaptychia ciliaris* f. *nigrescens* n. f., *Xanthoria microspora* n. sp., *Caloplaca mortariicola* n. sp., *Pyrenodesmia variabilis* v. *cyclysca* n. v., *Aspicilia hoffmannii* v. *muricola* n. v., *Lecidea moritzii* nom. nov. for *L. cacuminum* B. de Lesd. non Magn.]

BUGNON, F. Observations sur quelques lichens silvatiques nouveaux ou peu connus en Côte-d'Or. Bull. Sci. de Bourgogne 17: 11-15. 1956.

CHOISY, M. La systématique du genre *Ramalina* Ach., lichens discomycètes ascohyméniales. Bull. Soc. Mycol. France 73(2): 179-188. 1957.

———. Tableau d'une classification "archéophylétique" des Ascolichens. Bull. Soc. Bot. France 104(5-6): 330-338. 1957. [New: *Dendrographa* sect. Darbishirella (Zahl.) n. c., *D. gracillima* (Kremp.) n. c., *D.* sect. Roccellaria (Darb.) n. c., *D. mollis* (Hampe) n. c., *D.* sect. Ingaderia

[1] Names of new taxa from the Americas are marked with an asterisk (*).

[2] Dept. of Botany, Duke University, Durham, N. C.

[3] Names and titles transliterated and translated respectively from the Russian.

[4] Names and titles translated from the Japanese.

(Darb.) n. c., *D. pulcherrima* (Darb.) n. c. *Roccella* sect. Pentagenella (Darb.) n. c., *R. fragillima* (Darb.) n. c., *R.* sect. Reinkella (Darb.) n. c., *R. lirellina* (Darb.) n. c.; *Evernia poeppigii* (Nees & Flot.) n. c., *E. lethatiiformis* (Mot.) n. c., *E. malacea* (Stirt.) n. c., *E. duseni* (DR.) n. c., *E. alectoroides* (Mot.) n. c., *E. oxygona* (Mot.) n. c., *E. cladonioides* (Nyl.) n. c., *E. intricata* (Moris) n. c., *E.* sect. Letharia (Hue) n. c., *E.* sect. Everniopsis (Nyl.) n. c., *E. cirrhata* (Fr.) n. c.; *Ramalina* sect. Protoramalina (Choisy) n. c.]

CULBERSON, W. L. *Parmelia caroliniana* Nyl. and its distribution. Jour. Elisha Mitchell Sci. Soc. 73(2): 443-446. 1 *fig.* 1957.

DAMMAN, A. W. H. The South-Swedish Calluna-heath and its relation to the Calluneto-Genisetetum. Bot. Not. 110(3): 363-398. 7 *fig.* 6 *tab.* 1957. [Several lichens and bryophytes.]

DANIELSEN, A. Survey of Havaas' exsiccata. *Pp. 22-29 in* J. Havaas, "Notes on the lichen flora of the mountains Steinsaeterhorgi and Smøreggfjellet in Granvin. Hordaland tylke (W. Norway)." Univ. i Bergen Årbok 1954 (Naturvitensk. rekke Nr. 12): 1-29. 1954.

EHRENSVÄRD, G. Precursors and related compounds in the biosynthesis of aromatic amino acids.—A survey. Svensk Kem. Tidskr. 66: 249-268. 7 *fig.* 2 *tab.* 1954. [Lichen substances, p. 261.]

ERVI, L. O. & H. SALTIN. Kangasraunikin, *Gypsophila fastigiata* L., esiintymisestä Satakunnassa. Arch. Soc. Zool. Bot. Fenn. 'Vanamo' 8: 105-109. 1 *fig.* 1953. [6 lichens, 2 bryophytes.]

GELTING, P. *Parmelia subaurifera* Nyl. and *P. fraudans* (Nyl.) Nyl. in Greenland. Friesia 5(3-5): 240-246. 1 *fig.* 1956.

GUILLAUMIN, A., F. MOREAU, C. MOREAU. La Vie des Plantes. 1-472 *pp. illus.* Librairie Larousse. Paris. 1955. [Lichens, pp. 233-238; bryophytes, pp. 239-245.]

HAKULINEN, R. Lichenotheca Fennica a Museo Kuopioënsi Edita. Schedae ad Fasciculos XXXVI-XXXVIII (Nr. 876-950). *27 pp.* Kuopio. 1957. [Labels for nos. 876-950 in this exsiccata.]

HALE, M. E. JR. Corticolous lichen flora of the Ozark Mountains. Trans. Kansas Acad. Sci. 60(2): 155-160. 1957. [63 spp.]

HÄYRÉN, E. Veli Räsänen. Mem. Soc. pro Fauna et Flora Fenn. 30: 85-86. (1953-1954) 1955. [Necrological.]

HENRIKSSON, ELISABET. Studies in the physiology of the lichen *Collema*. I. The production of extracellular nitrogenous substances by the algal partner under various conditions. Physiol. Plantarum 10(5): 943-948. 1 *fig.* 1 *tab.* 1957.

IMSHAUG, H. A. Alpine lichens of western United States and adjacent Canada. I. The macrolichens. THE BRYOLOGIST 60(3): 177-272. 2 *fig.* 85 *maps.* 1957. [Many spp.; keys. New: *Stereocaulon subalbicans** Lamb n. sp., *S. depreaultii* v. *caespitosulum* (Nyl.) Lamb n. c.; *Umbilicaria lambii** n. sp., *U. coriacea* nom. nov. for *Gyrophora rigida* DR. non Hoffm., *U.* sect. Decussatae (Schol.) n. c., *U. kraschenninikovii* v. *darowii* (Frey) n. c.; *Dactylina madreporiformis* f. *sorediata** n. f.]

———. The lichen genus *Pyxine* in North and Middle America. Trans. Amer. Micros. Soc. 76(3): 240-269. 15 *fig.* 1957. [13 spp. Key. New: *P.* subsect Astipitatae* n. subsect., subsect. Rubrostipitatae* n. subsect., sect. Phragmopyxine (Clem.) n. c.; *P. berteriana* (Fée) n. c. with v. *subobscurascens* (Malme) n. c., *P. physciaeformis* (Malme) n. c., *P. isidiophora* (Müll. Arg.) n. c., *P. caesiopruinosa* (Tuck.) n. c., *P. pringlei** n. sp.]

[Kobayashi, M.][4] [Geographical range of *Gyrophora esculenta* in Pref. Fukushima.] Misc. Bryol. et Lichen. [Japan] 9: 2. 1 *map*. 1957.

[Kortchagin, A. A.][3] [Influence of fire on forest vegetation and its regeneration after fire in northern Europe.] Geobotanica [Akad. Nauk SSSR, Bot. Inst. Trudy ser. 3] 9: 75-149. 5 *fig*. 26 *tab*. 1954. [Including the regeneration of lichen and moss vegetation.]

[Kurokawa, S.][4] [Habitats of some lichens.] Misc. Bryol. et Lichen. [Japan] 11: 1. 1957. [On *Pannaria stylophora* Vain., *Sticta argyracea* Del. and *Parmelia enteromorpha* Ach.]

[———].[4] [A collecting trip of lichen at Hakone.] Misc. Bryol. et Lichen. [Japan] 12: 5. 1957. [24 spp.]

Kut'ák, V. Lišejníky v Krkonoších. [Die Flechten im Riesengebirge.] Časopis Nár. Mus. 121: 106-116. 1952. [Many spp.]

Lange, O. L. Zur Methodik der kolorimetrischen CO_2-Bestimmung nach Älvik. Ber. Deutsch. Bot. Gesell. 69(2): 49-60. 6 *fig*. 1956. [Mention of *Peltigera praetextata* and *Cladonia rangiferina*.]

———. Die Flechte *Parmelia paraguariensis* als Handelsware in der südlichen Sahara. Natur & Volk 87(8): 266-273. 7 *fig*. 1957.

Lettau, G. Flechten aus Mitteleuropa XII. Feddes Repert. 59(3): 192-257. 1957. [Parmeliaceae and Usneaceae; spp. nos. 1540-1699. New: *Parmelia stenophylla* f. *imbricata* (Mass.) n. c., f. *taeniata* (And.) n. c., v. *vagans* (Nyl.) n. c.; *Cornicularia aculeata* v. *muricata* f. *minutella* (Harm.) n. c.]

Luttrell, E. S. The ascostromatic Ascomycetes. Mycologia 47: 511-532. 2 *fig*. 1955. [Including some lichen classification.]

Railonsala, A. Lappfjärdin jäkäliä. [Flechten aus Lappfjard im westlichen Mittelfinnland.] Arch. Soc. Zool. Bot. Fenn. 'Vanamo' 9: 108-114. (1954) 1955. [198 spp., 52 vars., 37 forms.]

Ritchie, J. C. A plant collection from northwestern Manitoba. Canad. Field-Nat. 70(4): 171-181. 1 *fig*. 1956. [22 lichens, 40 bryophytes.]

———. The vegetation of northern Manitoba. I. Studies in the southern spruce forest zone. Canad. Jour. Bot. 34: 523-561. 13 *fig*. 8 *tab*. 1956. [Several lichens.]

Sato, M. Lichens of the Okuhyuga area. Jour. Hattori Bot. Lab. 13: 36. 1955. [19 spp.]

———. Range of the Japanese lichens (I). Bull. Fac. Liberal Arts, Ibaraki Univ., Nat. Sci. 6: 27-38. 11 *fig*. 1 *pl*. 1956. [5 spp. New: *Gyrophora kisovana* Zahl. n. sp.]

———. Range of the Japanese lichens (II). *Ibid*. 7: 57-69. 20 *fig*. 1957. [10 spp.]

[———].[4] [On a list of Lichenes from Ibaraki Pref.] Misc. Bryol. et Lichen. [Japan] 11: 4. 1957. [5 spp.]

[———].[4] [Lichen flora of mts. Ominesan and Odaigaharayama.] *Ibid*. 13: 1. 1957.

[———].[4] [A new habitat for *Dermatocarpon myogiense*.] *Ibid*. 9: 3-4. 1957.

Sbarbaro, C. Aliae Lichenum species in Italia (praesertim in Liguria) inventae annis 1941-1955. Ann. del Mus. Civ. di Storia Nat. di Genova 68: 259-288. 1956. [List of spp. 270-781. Previous part: *Ibid*. 61: 18-49. 1941.]

Sm[ith], A. L[orrain] [with additions by] G. G. N[earing]. Lichens. Encycl. Brit. 14: 29-34. 19 *fig*. 1957.

Söyrinki, N. Über die Relikvorkommnisse von *Poa glauca* Vahl in Süd-

finnland. Arch. Soc. Zool. Bot. Fenn. 'Vanamo' 9(Suppl.): 354-375. 10 *fig.* 1955. [6 lichens, many bryophytes.]

SUBRAMANIAN, S. A review of anthraquinone compounds in lichens. Jour. Amer. Pharm. Assoc., Sci. Ed. 44: 769-776. 3 *charts.* 1955.

SZATALA, Ö. Prodrome de la flore lichénologique de la Nouvelle Guinée. Ann. Hist.-Nat. Mus. Nationalis Hungarici (ser. nov.) 7: 15-50. (1955) 1956. [224 spp. Keys. New: *Arthopyrenia novae-guineae* n. sp., *A. birói* n. sp., *Leptorhaphis novae-guineae* n. sp., *Pseudopyrenula limitata* n. sp., *Clathroporina birói* n. sp., *Pyrenula ochracea* n. sp., *P. rubidopunctata* n. sp., *Phacotrema microcarpa* n. sp., *Leptotrema argillaceum* n. sp., *L. bisporum* n. sp., *Leptogium incavatum* n. sp., *Sticta pedunculata* v. *parvula* n. v., *Cyanisticta semilianata* v. *epunctulata* n. v., *Stictina fimbriata* v. *calvescens* n. v., *Lecanora dispersogranulata* n. sp.]

[TAKAMIZU, N.][4] [Geographical range of *Gyrophora esculenta* in Tokyo pref.] Misc. Bryol. et Lichen. [Japan] 12: 3-4. 1957.

TAVARES, C. N. "*Teloschistes bioreti* Des Abb." and the variation in *Anaptychia intricata* (Desf.) Mass. Portugaliae Acta Biol. (B) 6(1): 44-52. 6 *fig.* 1957. [*T. b.* = *A. i.*]

TOBOLEWSKI, Z. Materiały do flory porostów Tatr II. [Materials to the lichen flora in the Tatra Mountains II.] Poznańskie Towarzystwo Przyjaciół Nauk, Wydz. Mat.-Przyrodniczy 12 (Plantae Cryptogamae, Zeszyt 4): 1-22. 2 *fig.* 1957. [104 spp. English summary.]

VĚZDA, A. Lichenes Bohemoslovakiae Exsiccati, Editi ab Instituto Botanico Universitatis Agriculturae et Silviculturae, Brno, ČSR. Fasciculus IV. Dec. 10-12 (1957). 8 *pp.* 1957. [Labels for nos. 91-120 in this exsiccata.]

WERNER, R.-G. Notes de lichénologie libano-syrienne. IV. Bull. Soc. Bot. France 104(5-6): 321-326. 1957. [33 spp. New: *Pertusaria sublecanorodes* n. sp.]

NEWS AND NOTES

THE STARTING DATE FOR MUSCOLOGICAL NOMENCLATURE. In the last issue of THE BRYOLOGIST, in "News and Notes," the statement appears that, "A further discussion of the starting date for moss nomenclature at the Stanford meetings showed the order of preference to be Jan. 1, 1801, April 1801, Dec. 31, 1801." Actually, there was no formal discussion of this problem at the Stanford meetings other than a report by myself that the British Bryological Society had scheduled at its next annual meeting a discussion of the entire issue. Unfortunately, a report of their decision is still unavailable.

The American Bryological Society did consider this problem at its Storrs meeting, 27 August 1956. According to the minutes taken by myself, the resolution which was passed unanimously by those members present was as follows: "Regarding the action of the International Botanical Congress in declaring the date of publication of Hedwig's *Species Muscorum* to be 31 December 1801: *a.* WHEREAS by this action several important and widely used books of 1801 are placed before the starting point of moss names, and WHEREAS it seems probable that more, rather than fewer, changes in nomenclature will be called for by the new rule, THEREFORE, be it resolved that the American Bryological Society requests the Committee on Bryophytes of the International Botanical Congress to reconsider its decision re-

garding the starting date of moss names so that some conclusion acceptable to a majority of bryologists may be reached. *b.* The preferred date for the starting point of muscological nomenclature is according to the following sequence: 1'st, 19 April 1801 (The actual date of publication of the *Species Muscorum*); 2'nd, 1 January 1801; 3'rd, 31 December 1801."

Subsequently, under "News and Notes" in *Taxon* [6(2):55], Dr. R. van der Wijk, in behalf of the Committee for Bryophytes, called for an expression of opinion from bryologists to help the committee come to a proper decision in this controversy. Anyone who has definite and considered opinions concerning this problem is urged to write to Dr. van der Wijk immediately. The importance of coming to the wisest decision in this matter can hardly be overstressed in view of the fact that the new *Index Muscorum* is already in preparation.—L. F. KOCH.

In November WALTER J. EYERDAM went to southern Chile to collect plants for the botanical gardens of the University of California. He planned also to make general botanical collections. RUTH D. SVIHLA has been spending the "summer" in New Zealand collecting bryophytes for the herbarium of the University of Washington; her work has been aided by a university grant. GENEVA SAYRE planned to leave for Europe on March 4 to continue her bibliograpic studies on early bryological publications; she plans to return home about July 15. H. L. BLOMQUIST is spending six months at the Institute of Marine Biology, University of Puerto Rico (at Mayagüez), where he is working on marine algae.

RUDOLPH M. SCHUSTER will teach the course in archegoniates at the first session of the Mountain Lake Biological Station, Virginia (June 12-July 17). The course will be organized largely around field work and will deal primarily with the bryophytes. A. J. SHARP has taken leave of absence from the University of Michigan Biological Station at Cheboygan, and HOWARD CRUM will teach bryology and lichenology in his place (June 21-Aug. 16); inquiries should be addressed to Dr. A. H. Stockard, Dept. of Zoology, University of Michigan, Ann Arbor.

WILLIAM C. STEERE, presently dean of the graduate school at Stanford University, has been appointed director of the New York Botanical Garden to replace Dr. William J. Robbins, who retired Dec. 31. Dr. Steere will take office July 15. CLARK T. ROGERSON, formerly of Kansas State College, replaced Donald P. Rogers on Feb. 1 as curator of cryptogams at New York, and ROSALIE WEIKERT, long associated with the cryptogamic herbarium, has recently resigned.

LEO F. KOCH, director of the Hepatic Exchange, reported for 1957 a membership of 30. From an accumulation of 2366 specimens, 120 were deposited in the ABS herbarium and 1134 distributed to members. The Moss Exchange, under the direction of E. H. KETCHLEDGE, offered a choice of 455 specimens to members on the most recent exchange list. Such a large and interesting selection was made possible by the transfer of all the accumulated specimens from James Kucyniak, the former director. Keen interest in the moss exchange is evidenced by the fact that of nearly 600 packets offered on the previous list, less than 50 were left undistributed. (Information on membership in both exchanges may be found on the cover.)

Plans for the bryological and lichenological programs at the Ninth International Botanical Congress at Montreal (Aug. 15-29 1959) are

still preliminary. HOWARD CRUM is chairman of the subcommittees concerned with the bryological program and excursion, and JAMES KUCYNIAK is serving on both committees. A questionnaire was sent to 730 persons interested in bryology. Returns have been fairly good, but recipients are again urged to return the questionnaires *even if they do not expect to attend or will not be primarily interested in the bryological sessions.* With *your* cooperation, intelligent planning will become a possibility! At least one bryological excursion, probably in southern Quebec, is under consideration, and, of course, many other botanical tours in all parts of Canada will be open to bryologists. The subcommittee on lichenology includes MASON E. HALE, JR., chairman, RONALD E. BESCHEL, WM. L. CULBERSON and ROLF SANTESSON. A trip to New Brunswick and the Cape Breton area is being planned.

THE BRITISH LICHEN SOCIETY: On February 1st last the inaugural meeting of the British Lichen Society was held at the British Museum (Natural History). About 24 people attended the meeting at which it was reported that about 50 had already agreed to support the Society. The following officers were elected: Secretary: A. E. WADE, Dept. of Botany, National Museum of Wales, Cardiff; Treasurer: J. H. G. PETERKEN, 73 Forest Drive East, Leytonstone, London, E. 11; Editor: P. JAMES, Cryptogamic Botany Dept., British Museum (Natural History), Cromwell Road, London, S.W. 7; Librarian: D. C. SMITH, University Dept. of Botany, South Parks Road, Oxford; Recorder: P. JAMES, Cryptogamic Botany Dept., British Museum (Natural History), Cromwell Road, London, S.W. 7; Curator: T. D. V. SWINSCOW, "Everley," London Road, Knebworth, Herts. The annual subscription is £1; junior membership 10s; and family membership 5s. No decision was taken at the meeting concerning the publication of an annual report, but it is intended to issue a mimeographed bulletin from time to time.—A. E. WADE.

The annual business meeting and field excursion of BBS will be held at Haverfordwest, Pembrokeshire, April 3-9, 1958, with excursions by hired coach each day, to Canaston (Apr. 4), St. Davids (Apr. 5), Slebech and Picton Parks (Apr. 6), Saundersfoot and Ambroth (Apr. 9). On Sept. 13-20, a second meeting will be held at Barnard Castle, County Durham, with excursions headed by Dr. C. D. Piggott (Dept. of Botany, The University, Sheffield 10).

The Eighth Annual Wildflower Pilgrimage will be held in the Great Smokies, April 24, 25, 26, 1958. It is sponsored jointly by the Department of Botany of the University of Tennessee and the Gatlinburg Chamber of Commerce in cooperation with the Naturalist Service of the Great Smoky Mountains. The program includes short and long hikes, motorcades, photographic trips and illustrated evening lectures. Details can be obtained by writing the Chamber of Commerce, Gatlinburg, Tennessee. (The moss trip will be led by A. J. Sharp on Saturday, April 26.)

ZENNOSKE IWATSUKI finished his master's thesis on "Correlations between the Moss Floras of Japan and of the Southern Appalachians" (March 15, University of Tennessee) and planned returning to the Hattori Botanical Laboratory about April 1.

The next annual meeting of ABS will be held in conjunction with AIBS at Bloomington, Indiana, Aug. 24-28. Winona Welch will serve as

our local representative on the planning committee.

The Reverend ALPHONSE LUISIER died on November 4 of last year at Caldas da Saude (Portugal) at the age of 85. Father Luisier was an excellent collector and made noteworthy contributions to the bryofloras of Spain, Portugal and Madeira.

The compilation of an *Index Muscorum* is progressing steadily. The majority of names is now in the card index, and we are checking the names in the literature. Unfortunately not all papers are in Dutch libraries, and so for non-European mosses we need the help of bryologists of other regions. We have already received many reprints, and many bryologists have been most helpful. If an author wants the names of his new species or new combinations to be inserted properly, he might do well to send us a list of them, giving the places and dates of publication.

The *Index Muscorum* will be composed of four to five volumes, with 500-600 pages each. It is now clear that it cannot be finished before the next International Botanical Congress, but the editors will try to issue volume one before that time.—R. VAN DER WIJK.

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